

***Oenothera harringtonii* Wagner, Stockhouse &
Klein (Colorado Springs evening-primrose):
A Technical Conservation Assessment**



**Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project**

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COVER PHOTO CREDIT

Oenothera harringtonii (Colorado Springs evening-primrose). Photograph by the author.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF *OENOTHERA HARRINGTONII*

Status

Oenothera harringtonii (Colorado Springs evening primrose or Arkansas Valley evening primrose) is endemic to south-central Colorado. The NatureServe Global rank for this species is imperiled (G2). It is also designated imperiled (S2) by the Colorado Natural Heritage Program. The USDA Forest Service Rocky Mountain Region designates *O. harringtonii* as a sensitive species.

Primary Threats

Habitat loss due to urbanization, road development projects, and resource extraction activities, especially quarrying and surface mining, is a substantial threat to *Oenothera harringtonii*. Since several known occurrences are near highways, roadside maintenance activities, such as herbicide use, may impact the several known occurrences that are near highways. Recreational use of habitat is a threat to at least one occurrence at a Colorado state park. Invasion of habitat by non-native plant species is a potential threat throughout the range of this non-competitive species. Two classes of weeds pose substantial problems. Noxious weeds, such as field bindweed (*Convolvulus arvensis*) and jointed goatgrass (*Aegilops cylindrica*), and escaped non-native species used for agriculture and restoration, such as sweetclover (*Melilotus* spp.) and Mexican-fireweed (*Kochia scoparia*), have both been recorded at current occurrences. Livestock grazing, especially during flowering and fruiting periods, is likely to reduce the reproductive output of this species. This is a significant threat because *O. harringtonii* relies on seed production rather than vegetative reproduction to maintain its populations. Long-term sustainability of *O. harringtonii* populations is also jeopardized by declines in pollinator populations. The small size of many populations confers susceptibility to local extirpation from genetic, demographic, and environmental stochasticities.

Primary Conservation Elements, Management Implications and Considerations

Oenothera harringtonii is a rare species endemic to south-central Colorado. Currently no management plan directly address its management, but one is being developed for a small portion of its habitat under a Memorandum of Agreement by the Federal Highways Administration, the U.S. Fish and Wildlife Service, Colorado Department of Natural Resources (DNR), Colorado DNR Division of Wildlife, Colorado Department of Transportation, and The Nature Conservancy. Because *O. harringtonii* grows in road cuts, on highway rights-of-way, and eroding shale slopes, it may tolerate some disturbance. It is hypothesized that the taxon might even need some level of disturbance for seed germination. However, there is little information on which to base predictions as to its response to specific disturbance types or levels. It may well be excluded from a community if disturbance is too large or too frequent. Another facet of disturbance is the increased likelihood of introducing invasive weeds. Control methods of such weeds pose their own problems. Herbicides, particularly those that target forbs, may also kill *Oenothera* species. Controlling weeds by mowing when *O. harringtonii* is neither in flower nor bearing fruit may be a viable option. Cultivation (tilling) is not a good alternative until the consequences of such large-scale disturbance are better understood. The effects of fire on this species must be evaluated. *Oenothera harringtonii* is adapted to barren shale and gravelly areas that historically are unlikely to have experienced much litter accumulation. Therefore, unlike typical grassland species, its habitat likely only experienced infrequent, cool-temperature burns. Maintaining abundant and healthy populations of appropriate pollinators, such as *Hyles* species of hawkmoth and bees, is vitally important to population sustainability because *O. harringtonii* is an obligate out-crossing species.

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INTRODUCTION

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), USDA Forest Service (USFS). *Oenothera harringtonii* (Colorado Springs evening primrose or Arkansas Valley evening primrose) is the focus of an assessment because it is a rare species that is endemic to south-central Colorado and because the USDA Forest Service Region 2 has designated it as a sensitive species (Spackman et al. 1997, USDA Forest Service 2003). A sensitive species is a plant or animal whose population viability is identified as a concern by a Regional Forester because of significant current or predicted downward trends in abundance and/or in habitat capability that would reduce its distribution (FSM 2670.5 (19)). A sensitive species may require special management, so knowledge of its biology and ecology is critical.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, research biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species based on available scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop specific management recommendations. Rather it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications). Furthermore, this assessment cites management recommendations proposed elsewhere and examines the success of those recommendations that have been implemented.

Scope

This assessment examines the biology, ecology, conservation status, and management of *Oenothera harringtonii* with specific reference to the geographic and ecological characteristics of USFS Region 2. Although some of the literature relevant to the species originates from field investigations outside the region, this document places that literature in the ecological and social context of the central Rocky Mountains. Similarly, this assessment is concerned with the reproductive behavior, population dynamics, and

other characteristics of *O. harringtonii* in the context of the current environment rather than under historical conditions. The evolutionary environment of the species is considered in conducting this synthesis, but it is placed in a current context.

In producing this assessment, I examined refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on *Oenothera harringtonii* may have been referenced in the assessment, but an effort was made to consider all relevant documents. Refereed or peer-reviewed literature is preferred because it is the accepted standard in science. In cases where information was unavailable elsewhere, non-refereed publications and reports were used. These should be regarded with greater skepticism. However, many reports or non-refereed publications on rare plants are often reliable sources of information. They may be ‘works-in-progress’ or isolated observations on phenology or reproductive biology. For example, demographic data may have been obtained during only one year when monitoring plots were first established. Insufficient funding or manpower may have prevented work in subsequent years. One year of data is generally considered inadequate for publication in a refereed journal but still provides a valuable contribution to the knowledge base of a rare plant species. Unpublished data (for example, Natural Heritage Program and herbarium records) were important in estimating the geographic distribution and population sizes of this species. These data required special attention because of the diversity of persons and methods used in their collection. Records that were associated with locations at which herbarium specimens had been collected at some point in time were weighted more heavily than observations only.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, in the ecological sciences, it is difficult to conduct experiments that produce clean results. Often, observations, inference, good thinking, and models must be relied on to guide our understanding of ecological relations. Confronting uncertainty then is not prescriptive. In this

assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate.

One element of uncertainty often lies with confirming that the taxon is indeed rare. There is always the possibility that additional surveys would reveal more occurrences. When most information has been collected relatively casually, a criticism with defining a taxon as rare is that there are extensive areas as yet unsurveyed. To some extent this is true, but rarity is also relative, and many taxa are regarded as not being rare precisely because casual observation has noted that they occur frequently.

Publication of Assessment on the World Wide Web

To facilitate the use of species assessments in the Species Conservation Project, they are being published on the Region 2 World Wide Web site. Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More important, it facilitates their revision, which will be accomplished based on guidelines established by Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer reviewed prior to their release on the Web. This assessment was reviewed through a process administered by the Center for Plant Conservation employing at least two recognized experts on this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Oenothera harringtonii is endemic to south-central Colorado. The NatureServe Global rank (2001) for this species is imperiled (G2), and it is designated imperiled (S2) by the Colorado Natural Heritage Program (see “Rank” in Definitions section). The USDA Forest Service Rocky Mountain Region designated it as a sensitive species (USDA Forest Service 2003). A sensitive species indicates that it “is a plant species identified by the Regional Forester for which population viability is a concern as evidenced by a significant

current or predicted downward trend in population number or density and/or a significant current or predicted downward trend in habitat capability that would reduce a species’ existing distribution” (USDA Forest Service 2003). The sensitive designation requires that a documented biological evaluation to determine potential impacts to the species must be completed prior to any major project on National Forest System land (USDA Forest Service 1995). The goal is to avoid or to minimize impacts to sensitive species. *Oenothera harringtonii* is not designated a sensitive species by the Colorado State Office of the Bureau of Land Management, and therefore it has no protections on public land managed by that agency (Bureau of Land Management 2000).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Oenothera harringtonii occurs on National Forest System (NFS) lands managed by the USFS, on public lands managed by the BLM, and on lands managed by the Department of Defense (DoD), and the Colorado Department of Transportation (CDOT). The majority, at least 65 percent and likely more, of occurrences have been found on private land (**Table 1**). Only one occurrence has been found on National Forest System lands.

Several formal surveys targeting rare species, including *Oenothera harringtonii*, have been conducted on land managed by the USFS (Hazlett 1997, Hazlett 2000), BLM (Brekke personal communication 2003), and DoD (Shaw et al. 1989). There are currently no management plans that specifically address the management of this species. A Memorandum of Agreement among CDOT, the Federal Highway Administration, the U.S. Fish and Wildlife Service, Colorado Department of Natural Resources (DNR), Colorado DNR Division of Wildlife (CDOW), and The Nature Conservancy (TNC) has been signed to promote a proactive approach to conserving several rare and endemic species of the prairie, including *O. harringtonii* (Federal Highways Administration et al. 2002, updated 2004). As part of this “Shortgrass Prairie Initiative,” CDOT is developing “best management practices” to address issues of minimizing the impacts of road widening and road and right-of-way maintenance on sensitive species, including *O. harringtonii* (Powell personal communication 2003). An occurrence at the Pueblo Reservoir State Wildlife Area has been found on land managed by the Colorado State Parks. This

Table 1. Occurrences of *Oenothera harringtonii*.

Arbitrary Occurrence		Location	Dates Observed*	Land Management	Source
Number	County				
1	Alamosa	Wash Springs, San Luis Valley.	July 1897	Unknown	<i>E. Bethel s.n.</i> CS
2	El Paso	Colorado Springs.	May 29, 1939	Unknown	<i>J.H. Ehlers 7461</i> NY (Isotype)
3	El Paso	19 miles outside of Colorado Springs on Highway 115.	May 10, 1969	Bureau of Land Management (BLM) or private	<i>R. Simpson s.n. with S. Gardner</i> COLO
4	Fremont	1988: Blue Heron Property - BLM (Brekke personal communication). 2001: Steep slopes above Route 115 just northeast of Arkansas River crossing. 2003: Along Highway 120. Occurrence distributed over two sections.	May 29, 1998; July 22, 2001; May 21, 2003	BLM, State (highway right-of-way) and possibly private	<i>S. Spackman SS0106A</i> 2001 COLO. Colorado Natural Heritage Program (2002). Author's observation 2003
5	Fremont	1970: At junction of Highways 115 and 50. 1995: Penrose. Intersection of Highways 115 and US 50. 1999: US 50 and COLO 115.	May 22, 1970; June 3, 1995; June 16, 1999	Private	<i>D. Duba 15</i> 1970 COLO. <i>C. Crawford s.n.</i> 1995. COLO. <i>C.L. Crawford s.n.</i> 1999
6	Fremont	North of Highway 50, near the Gold Belt National Back County Byway.	June 14, 2000	Private	Colorado Natural Heritage Program (2002)
7	Fremont	15 miles northeast of Cañon City.	May 28, 1954	BLM and/or private and/or State of Colorado	<i>H. Harrington 7302</i> CS
8	Fremont	0.5 miles south of Florence on Highway 67.	July 2, 1967	Private	<i>R. Goeken 18</i> CS (triplicate specimens)
9	Fremont	1942: Arkansas River Canyon, 2 miles east of Concrete, near Pueblo County line. 1998: search along Highway 150 in general vicinity of 1942 site.	June 12, 1942; 1998	Private	<i>J.A. Ewan 14195</i> 1942 COLO. 1998 survey in Colorado Natural Heritage Program (2002)
10	Huerfano	About 8 miles south of Walsenburg, on west service road for I-25, 0.8 mile north of exit 42 (Pryor Exit).	May 26, 1995	Private	<i>W.F. Jennings 95-18 with R.E. Jennings</i> COLO
11	Las Animas	1993: Hwy I-25, near Exit 41, 29 miles N of Trinidad, on steep clay road cuts.	June 13, 1993; 1995; May 26, 1998	BLM and/or private	<i>Weber 18665 with Wittmann</i> 1993 COLO (duplicate specimens). Colorado Natural Heritage Program (2002)

Arbitrary Occurrence Number	County	Location	Dates Observed*	Land Management	Source
12	Las Animas	Approximately 1.5 miles west-northwest of Branson within 2 miles of the Colorado-New Mexico State line. Approximately 3 miles east-southeast of Walts Corner.	May 27, 1998	Private	Colorado Natural Heritage Program (2002)
13	Las Animas	Pinyon Canyon Maneuver Site, 3 miles north of Rd 2, NW of Joela Windmill.	May 28, 1997	Department of Defense	<i>T. Kelso 97-42 COLO</i>
14	Las Animas	Near road leading to ranch west of Trinchera, 1 mile from New Mexico-Colorado border.	June 11, 1968	Private	<i>R. Walter 1452 CS</i>
15	Las Animas	Along US 160, 3 miles northwest of western end of Mesa de Maya.	May 19, 1948	Unknown	<i>C.M. Rogers 5751</i>
16	Otero	North of David Canyon Road.	June 2, 1995	USDA Forest Service – Comanche National Grassland	<i>D.L. Hazlett 9471 COLO. Hazlett (1997).</i> Colorado Natural Heritage Program (2002)
17	Otero	North of Bloom within 0.5 km of the border of the USDA Forest Service Comanche Grassland.	May 24, 1997	Private	Colorado Natural Heritage Program (2002)
18	Otero	Rocky Ford, bank of Arkansas River.	June 13, 1891	Unknown	<i>C. Crandall s.n. 1981 CS</i>
19	Otero	Cedar mesas, 25 miles south of La Junta.	June 12, 1936	Unknown	<i>L. Paull 9 COLO</i>
20	Pueblo	West of Bragdon.	May 21, 1995	Private	<i>R. Hartman and T. Chumley 50265 1995 RM</i>
21	Pueblo	In town of Pueblo, east of junction between I 25 and Highway 50.	1897; June 03, 1931	Private	<i>A. Nelson 11527 1931 COLO in Colorado Natural Heritage Program (2002)</i>
22	Pueblo	Pueblo.	July 1897; 1908	Unknown	<i>E. Bethel s.n. 1897 COLO. W.W. Robbins 5022 1908 COLO</i>
23	Pueblo	Pueblo West, south of Highway 50.	July 17, 2001	Private	Colorado Natural Heritage Program (2002)
24	Pueblo	Just west of Pumpkin Hollow.	June 3, 1998; May 31, 2001	Private	Colorado Natural Heritage Program (2002)
25	Pueblo	North of Pueblo Reservoir.	July 19, 2001	Pueblo State Park	Colorado Natural Heritage Program (2002)

* Where only the year is reported, the day and month were unspecified.

occurrence is not experiencing active management at the present time (Mullis personal communication 2003, Tiemann personal communication 2003).

A small occurrence of *Oenothera harringtonii* was found during a preliminary survey for rare, threatened, and endangered plant species on the Comanche National Grassland (Hazlett 1997, Hazlett 2004). At that time, brief observations on the population size and habitat conditions were made. This occurrence is within a grazing allotment and may have experienced occasional prescribed fire (Olson personal communication 2004). *Oenothera harringtonii* appears on a working checklist of plant species on the grassland that was prepared in order to provide baseline information to land managers (Hazlett 2000, Hazlett 2004). USFS personnel consider the occurrence on the Comanche National Grassland when implementing management strategy of the area in which it occurs, but a plan specific to *O. harringtonii* has not been written and targeted surveys are not being conducted (Lammon personal communication 2003). *Oenothera harringtonii* is included in the document outlining general management strategies for selected sensitive plant species for the Grand Mesa, Uncompahgre, Gunnison, San Juan, Rio-Grande, Pike, and San Isabel national forests and Comanche and Cimarron national grasslands published by USDA Forest Service Region 2 (USDA Forest Service GMUG, SJ-RG, PISCC 1999).

Oenothera harringtonii populations are also on a part of the Fort Carson Military Reservation (Shaw et al. 1989). *Oenothera harringtonii* is not formally recognized as a species of concern on Fort Carson since it is not federally listed, but informal observations are made yearly on known populations (Rifici personal communication 2003). Plants are currently growing outside the area where most of the military maneuver activities are carried out, and thus there is little potential for catastrophic disturbance (Belew personal communication 2003).

Some *Oenothera harringtonii* occurrences are in areas with intensive mining activity, primarily for limestone for the cement industry. A preserve has been proposed in one of these areas (Colorado Natural Areas Program 1989, Carsey 1996). The preserve is specially designed to encompass occurrences of *Parthenium tetraeneuris* (Arkansa River feverfew), but it is unclear from the documents available if there are any extant populations of *O. harringtonii* within the proposed preserve boundary (Colorado Natural Areas Program 1989).

Biology and Ecology

Classification and description

Systematics and synonymy

Oenothera is a genus of the Onagraceae family that is commonly known as the evening primrose family. The genus *Oenothera* comprises at least 120 species, divided amongst 14 sections, distributed within North and South America (Gregory 1964a, Raven 1979, Levin 2004 et al).

Oenothera harringtonii is a member of the *O. caespitosa* complex within the subgenus (Stockhouse 1973) or section (Wagner et al. 1985) *Pachylophus*. An alternative (older) spelling of *Pachylophus* (Stockhouse 1973, Wagner et al. 1985) is *Pachylophis* (Munz 1931, Linsley et al. 1963). The section *Pachylophus* occupies an ancestral position within the genus *Oenothera* (Stockhouse 1973). Cleland (1957, 1972) and Raven (1962) outlined and concluded that the more ancestral condition within *Oenothera* was an outcrossing, self-incompatible, chromosomally structurally homologous, perennial, large-flowered, and many seeded taxon. The *O. caespitosa* complex comprises five species: *O. caespitosa*, *O. psammophila*, *O. harringtonii*, *O. cavernae*, and *O. brandegeei* (Wagner et al. 1985). There are also five subspecies of *O. caespitosa*: ssp. *crinita*, ssp. *caespitosa*, ssp. *navajoensis*, ssp. *macroglottis*, and ssp. *marginata* (Wagner et al. 1985).

Oenothera harringtonii is a taxon unique to Colorado. However, in the past it has been included with material from other states, and specimens have been labeled as various species of *Oenothera* and *Pachylophus*. Therefore the synonymous names can be quite confusing to those unaware that *O. harringtonii* has only relatively recently been recognized as a unique taxon. Synonyms for *O. harringtonii* include *O. caespitosa* Nutt. var. *eximia* (Gray) Munz pro parte (Munz 1931), *Pachylophus exiguus* (A. Gray) Rydberg pro parte (Rydberg 1903), *P. eximius* (A. Gray) Wooton and Standley pro parte (Wooton and Standley 1913). The term *pro parte*, which literally means “in part”, indicates that material used to initially describe the species in question included specimens of *O. harringtonii*. Specifically Rydberg (1903) grouped together specimens collected in Rocky Ford Colorado with those from New Mexico and Arizona. Similarly, Munz (1931) included *O. harringtonii* in his concept of *O. caespitosa* var. *eximia* using a specimen from Santa Fe Creek in New Mexico as the type specimen.

This type specimen was later designated that for *O. caespitosa* Nutt. ssp. *marginata*, which does not overlap the range of *O. harringtonii* (Wagner et al. 1985).

History of species

In 1849, Asa Gray first published a description of *Pachylophus eximia* (Gray 1849) that included specimens from central Colorado. Later, Rydberg (1903) included specimens of *Oenothera harringtonii* in his concept of *P. exiguus* (A. Gray) Rydb. In his notion of *P. exiguus* he included specimens from the White Mountains in New Mexico collected by Wootton in 1897 and also specimens from Walnut Canyon in Arizona collected in 1898. It is likely that the few specimens with which he had to work prompted him to combine them all to form one species. Munz (1931) later recognized *O. harringtonii* as a member of the *O. caespitosa* complex, and he included the specimens of *O. harringtonii* that he examined in his concept of *O. caespitosa* var. *exima*. Later, with more material with which to make comparisons, Wagner (1983) recognized it as a unique taxon and named it *O. harringtonii* in honor of Harold D. Harrington (1903-1981), a notable expert on Colorado flora.

Non-technical description

Oenothera harringtonii (**Figure 1**) is an annual or sometimes biennial species (Wagner et al. 1985). In some cases it has been reported to be a short-lived perennial (Weber and Wittmann 2001). However, the latter condition needs further confirmation. It has a stout taproot with one to five stems from a definite basal rosette. The stems are yellowish-fawn color, usually with reddish-purple splotches. They are 15 to 30 cm tall with both glandular and non-glandular hairs. The closely spaced leaves are green, thin, and also have non-glandular and glandular hairs. The hairs of both types are most dense along the margins and midrib. The leaves are tapering in shape, 10 to 14.5 cm long, and 1.5 to 3 cm wide with toothed margins. Sometimes the margins will be shallowly (6 to 8 mm long) lobed near the base of the leaf. The buds are erect without free sepal-tips. The flowers have a heavy fragrance. Generally five to ten flowers per stem open each day. The floral platform is nearly vertical. The petals are white, fading to pink, with a broad notch from 3 to 5 mm deep. The floral tube is 3.1 to 6 cm long. Each stem has from six to 20 capsules maturing on the stem. The capsule (fruit) is approximately 2.1 to 3.5 cm long by 5 to 8 mm in diameter and tapers to a 6 to 8 mm long beak at the end. The capsule is approximately quadrangular, rather than cylindrical, with tubercles or knobs on the

margins of the valves. There are 60 to 100 reddish-brown seeds per capsule. The seeds are 2 to 3.5 mm long. On the adaxial side of each seed, there is a hollow chamber that Wagner et al. (1985) termed a seed collar. This feature is unique to members of the *caespitosa* complex, of which *O. harringtonii* is part. The above description primarily uses information from Wagner et al. (1985). Photographs of *O. harringtonii* are provided in **Figure 2**.

Although *Oenothera harringtonii* is generally distinct from *O. caespitosa* in having robust, leafy stems, it should be noted that *O. caespitosa* also produces a stem under cultivation (Weber and Wittmann 2001, Wittmann personal communication 2003). One of the best distinguishing characteristics appears to be mature capsule morphology that is very consistent within the *O. caespitosa* group (Wagner et al. 1985, Goeken 1968). *Oenothera harringtonii* has quadrangular-shaped capsules that have particularly prominent knobs on the valve margins. Wagner et al. (1985) report that hair type also provides an excellent diagnostic characteristic to differentiate among the species in the *O. caespitosa* complex. As mentioned above, hairs on *O. harringtonii* are of two types: glandular and non-glandular (Wagner et al. 1985). The glandular hairs are tiny (0.1 to 0.2 mm long), erect, transparent, and they exude a drop of liquid. The non-glandular hairs are slender, unicellular, straight, and not perceptibly broadened at the base. This characteristic may not be completely infallible since Goeken (1968) suggests that there are problems associated with using a characteristic that may be under the control of a single gene.

Most members of the *Oenothera caespitosa* complex are separated either by geography or habitat requirement. The range of *O. caespitosa* ssp. *macroglottis* and *O. harringtonii* overlap in Fremont County, but because of the difference in their habitat requirements, they are seldom sympatric. They do, however, come into contact along the Arkansas River between Parkdale and Cañon City (Wagner et al. 1985). Characteristics that differentiate *O. harringtonii* from *O. caespitosa* ssp. *macroglottis* are described in **Table 2**.

References to technical descriptions, photographs, line drawings and herbarium specimens

A detailed technical description and line drawing of *Oenothera harringtonii* can be found in Wagner et al. (1985) and Spackman et al. (1997). Other comprehensive technical descriptions are published in Goeken (1968) and Stockhouse (1973). A key to the taxon is published

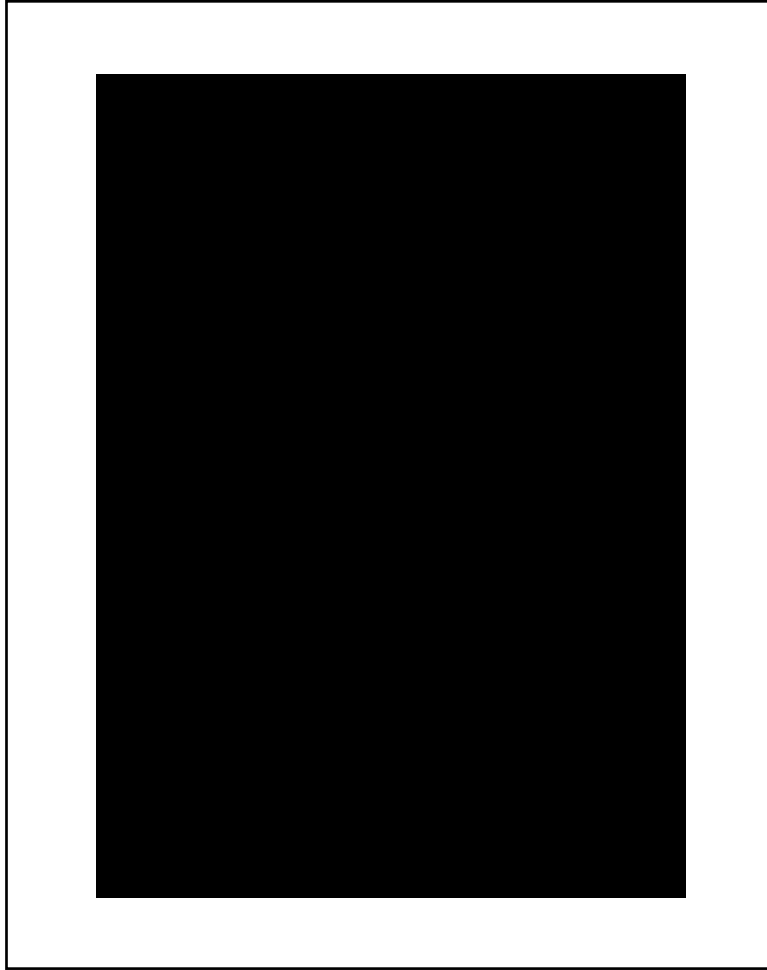


Figure 1. Illustration of *Oenothera harringtonii*. Illustration © by Janet Wingate; used with permission.

in Weber and Wittmann (2001). The holotype, collected by J.H. Ehlers 37461 in the Colorado Springs area in El Paso County in May 1939, is deposited in the University of Michigan herbarium, but only the label information is available on the Internet. A photograph of an isotype herbarium specimen (J. H. Ehlers 7461, 29 May 1939) collected from El Paso County, Colorado is on the New York Botanical Garden web page (2003). See the References section for Internet site addresses.

Distribution and abundance

Oenothera harringtonii is endemic to south-central Colorado (**Figure 3, Table 1**). It has been reported from El Paso, Fremont, Huerfano, Las Animas, Otero, and Pueblo counties. There is also a reference to it occurring in the San Luis Valley in Alamosa County in July 1987 (collected by Ellsworth Bethel, specimen accession number 26210 in the Colorado State University Herbarium). Approximately 33 documented

occurrences have been reported since 1891, but only 17 occurrences have been observed within the last 20 years. One of the more recently documented occurrences is on the Comanche National Grassland, and another is on private land within 0.5 km of the Comanche National Grassland border.

A population can be defined as “a group of individuals of the same species living in the same area at the same time and sharing a common gene pool or a group of potentially interbreeding organisms in a geographic area” (National Oceanic and Atmospheric Administration 2004). A less restrictive definition of population, and the one that is used in this report since the species’ genetics are unknown, is that it is “a group of individuals of the same species that occurs in a given area” (Guralnik 1982). In this report, occurrences (populations) include plants in large areas of land where there are contiguous stretches of apparently suitable, or potential, habitat. One occurrence of



Figure 2. Photograph of *Oenothera harringtonii*. The insert shows the flowers in more detail. Photograph taken at 9:45 a.m., May 21, 2003, by Juanita A. R. Ladyman.

Table 2. Characteristics of *Oenothera harringtonii* compared to those of *O. caespitosa* ssp. *macroglottis* (after Wagner et. al 1985, McGregor et al. 1986, Weber and Wittmann 2001).

Species	Stem	Capsule characters	Capsule pedicel (stalk)	Seed shape	Seed collar*	Flower	Floral tube length number in () is max
<i>Oenothera harringtonii</i>	caulescent; stems up to 30cm long	lanceoloid to ovoid capsules; large (2 to 3mm high) tubercles (knobs) on the angles of the capsules.	not an actual pedicel; broad constriction ~ half capsule diameter at base of capsule.	narrowly obovoid	distally sinuate and depressed	2 to 2.6 cm long x 2.7 to 3.3 cm wide with broad notch 3 to 5 mm deep.	3 to 7 (8.5) cm
<i>Oenothera caespitosa</i> ssp. <i>macroglottis</i>	acaulescent; stems 4 to 8 cm long	lance-cylindrical; wavy ridges rather than tubercles.	pedicel 4 to 7 mm long.	Obovoid	entire and narrow	2.1 to 5 cm long x 3 to 8 cm wide with broad shallow notch.	4.5 to 14 (16.5) cm

* micrographs in Wagner et al. (1985)

Oenothera harringtonii usually consists of several sub-occurrences (sub-populations). Interaction, through pollination or seed dispersal, is believed to occur between sub-occurrences. However, without knowing the seed dispersal range and specifics of its pollination biology it is very difficult to delineate what comprises a single interbreeding group of plants. In some cases a reported occurrence may be more accurately described as a sub-occurrence, but there may be insufficient information associated with the report to make an accurate delineation. For example, the population along the right-of-way of Highway 120 (Occurrence 4, [Table 1](#)) is likely composed of several sub-populations. Plants in this area were distributed along a stretch of at least 0.6 miles (author's personal observation 2003). Two stands (sub-populations) with three to five individuals each, on the north side of the road, were separated by approximately 0.15 miles, and they were approximately 0.45 miles away from a third sub-population of approximately 62 individuals that was located on the south side of the road. These three stands were clearly separate but are likely to interact, at least, via pollinator activity. If different observers had reported these stands, it is possible that they would have been recorded as one, two, or even three occurrences, instead of one occurrence composed of three sub-occurrences, depending upon the details of the location information.

Observations ranging from a single plant being counted at an occurrence to an estimated 100

individuals per occurrence have been reported. In some cases, 'several,' 'abundant,' or 'numerous' have been used to describe an occurrence. In general, occurrence size appears to be quite small. Reports of less than 10 individuals per occurrence appear to be common. However, small rosettes can be quite obscure, especially in areas with a moderate level of vegetative cover, and so they may have been overlooked. Even quite large plants may be cryptic. An observation was made that plants flowering one day were not noticed the previous day (Colorado Natural Heritage Program 2002). Sixteen occurrences comprising a total of approximately 360 plants (vegetative rosettes plus flowering adults) have been reported since 1990. Considering that there are likely several unreported occurrences on private land and that all occurrences reported within the last 20 years are extant, one can make an (optimistic) estimate that there are at least 20 extant populations. If there are between three and 100 (average 20) plants per population, a total of 400 plants may be currently growing within its limited range.

Occurrence data have been compiled from the Colorado Natural Heritage Program, and specimens at the University of Colorado Herbarium (COLO), Colorado State University Herbarium (CS), the Kathryn Kalmbach Herbarium at Denver Botanic Gardens (KHD), the Gray Herbarium at Harvard University (GH), the New York Botanical Garden Herbarium (NY), and from the literature (Goeken

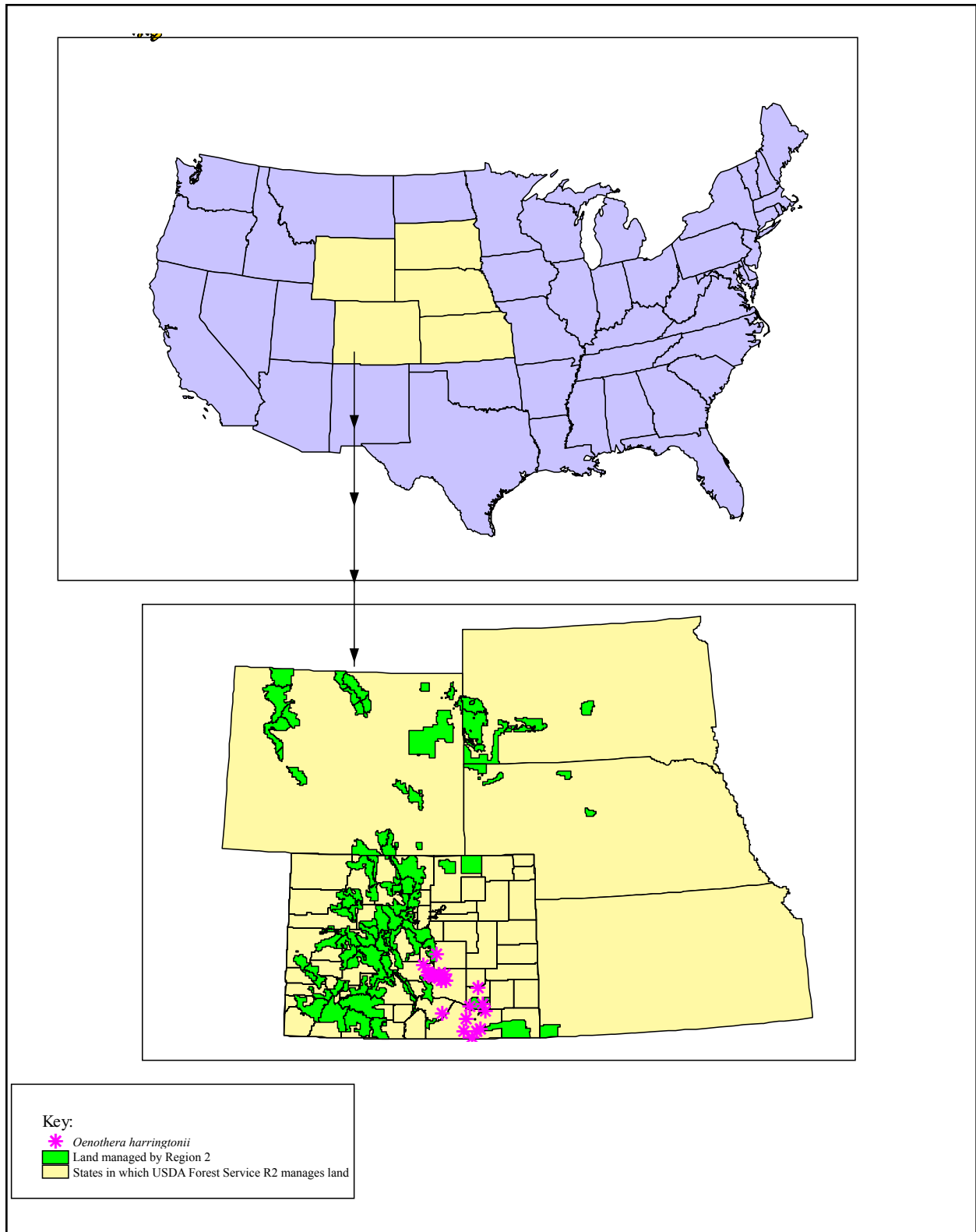


Figure 3. Range of *Oenothera harringtonii* based on occurrences records (Colorado Natural Heritage Program 2002), herbarium specimens, and the literature. National Forest System lands are shaded green.

1969, Stockhouse 1973, Wagner et al. 1985). It must be noted that many, particularly older, records do not have precise location information and errors may have been made in determining the exact number of occurrences. In some cases a site may have been revisited and designated a new occurrence, or discrete populations in the same general vicinity may have been estimated to be the same population.

Population trend

There are insufficient data in the literature, associated with herbarium specimens, or at the Heritage Programs to accurately determine population trends. Over the last 30 years there has been no critical quantitative monitoring, and only six sites have been recorded as being revisited within the last decade. Specific population locations were not clearly defined during the first visit, so only the same general areas were surveyed. Plants have persisted at five of the six sites. At three of the sites the time between visits was between three and five years (Occurrences 4, 11 and 24, [Table 1](#)). At the fourth site, the time between visits was approximately 30 years (Occurrence 5, [Table 1](#)), and at the fifth site the time interval was 56 years (Occurrence 9, [Table 1](#)). Therefore, it can be concluded that plants may persist over several decades in the same general area. No plants were found at the sixth site, but the original directions provided in 1942 were sufficiently vague that the actual site may have been elsewhere (Colorado Natural Heritage Program element occurrence records 2002). The occurrence observed in 1995 (Occurrence 16, [Table 1](#)) on the Comanche Grassland has not been relocated since that time although occasional surveys have been made in the area of the original occurrence (Olson personal communication 2004). Populations at Fort Carson have not been noticed for the last two years (Rifici personal communication 2003). Rifici (personal communication 2003) suggested that the drought of 2002 was responsible for the lack of plants. The drought may have killed mature plants and prevented germination of seed in the soil seed bank.

This taxon appears to occur infrequently and in small populations. There is little specific evidence to suggest it is either more or less common at the present time than in the past. However, one cannot say with certainty that it has not experienced a decline in the last century. Considerable habitat loss and fragmentation have occurred due to urban expansion, resource extraction activities, and recreational use (Carsey 1996). Therefore, the number of occurrences, if not the size of the individual occurrences, has most likely declined.

Habitat

Oenothera harringtonii grows at elevations between 1,400 and 2,000 m (4,600 and 6,600 feet) above sea level ([Figure 4](#)). The winters where *O. harringtonii* occurs tend to be dry. Annual precipitation averages approximately 330 mm, and 70 percent of that occurs from April through September (Laurenroth and Milchunas 1992). Typically plants are found on compacted, silty clay soil, but they may also grow on rocky, sandy, and silty loam soils (Colorado Natural Heritage Program 2002). It primarily colonizes the Niobrara formation that is composed of calcareous shale and limestone, Carlisle shale, Greenhorn limestone, Graneros shale, and Pierre shale formations (Tweto 1979). It is also found on the Purgatoire formation that is a mix of sandstone and shale and Dakota sandstone (Tweto 1979). Detailed analyses of the soil of two populations suggested that high amounts of silt were favored, but the proportional composition of clay and sand was less correlated. Soils at one site were composed of 32 percent sand, 60 percent silt, and 8 percent clay (Goeken 1968) while at another site soils were 29 percent sand, 48 percent silt, and 23 percent clay (Stockhouse 1973). The soils can also be highly seleniferous since a common associate is *Stanleya pinnata* (prince's plume), which typically grows on high-selenium clay soils (Welsh et al. 1993). Descriptions of habitat that were reported at each of the occurrence sites are listed in [Table 3](#).

In general, *Oenothera harringtonii* grows on almost flat ground or gentle slopes. In rarer cases, slopes of up to 30 degrees have also been colonized. Plants are most often found on barren shales and in disturbed areas such as on road cuts, in tire tracks, and along eroding slopes. Plants grow in full sun to partial shade. Apparently, no particular aspect is required although southern, southwestern, and southeastern aspects may be slightly favored. Both relatively mesic and, more commonly, xeric habitats are colonized. Plants grow in open grassland, specifically shortgrass prairie, or in *Atriplex* spp. (saltbush) shrub communities. At one occurrence, plants also extended into a *Sarcobatus vermiculatus* (greasewood) community. Some of its associated species are listed in [Table 4](#). This is not an exhaustive list and represents only the observations that were made on herbarium sheets, in Goeken (1968), by personal observation of the author, and in Colorado Natural Heritage Program element occurrence records (2002). Generally the plants appear to grow in areas with relatively low vegetation cover, from less than 20 to approximately 50 percent, but from these relatively

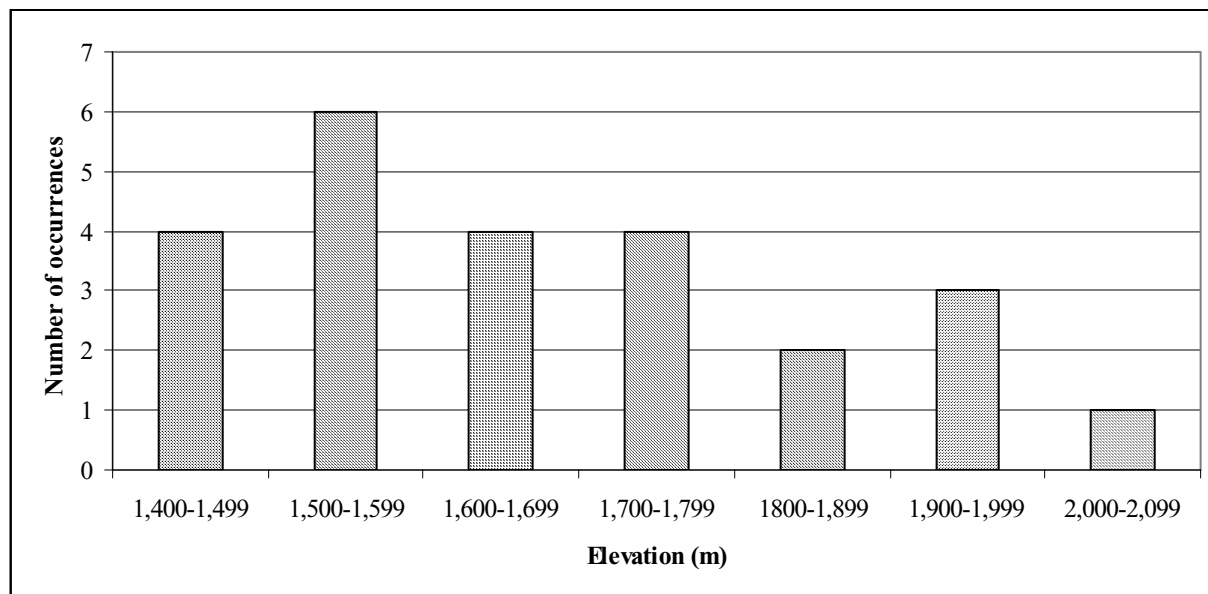


Figure 4. Range in elevation reported for the occurrences of *Oenothera harringtonii*. These elevations represent the observations that were made on herbarium sheets, in Goeken (1968) and Colorado Natural Heritage Program (2002). Where a range was indicated, the lowest and highest elevations were included in the graph.

Table 3. A summary of the habitat conditions for each occurrence in [Table 1](#).

Arbitrary Occurrence Number	Dates Observed	Habitat	Abundance and reproductive status	Comments
1	July 1897	No information.	No information.	No information.
2	May 29, 1939	Dry slopes in the foothills.	In flower.	No information.
3	May 10, 1969	Along a moist sandy fence line at 6,000 ft.	Reproductive status: flower and fruit.	Original id: <i>O. caespitosa</i> Nutt. Annotated <i>O. albicaulis</i> by W.A. Weber Dec 1993. Annotated <i>O. harringtonii</i> by W.L. Wagner .
4	May 29, 1998; July 22, 2001	2001: South to southwest facing slopes in shrubland with fine particle soils. River cobbles on surface of eroding shales. With <i>Atriplex</i> spp., <i>Frankenia jamesii</i> , <i>Oryzopsis hymenoides</i> .	2001: 10-20 plants in small area. Number of individuals counted: approximately 50; estimated population size: 100.	2001: Reproductive status: Fruit: 100 percent.
5	May 22, 1970; June 3, 1995; June 16, 1999	1970: Disturbed, alkaline soil with small eroded gulches at 5,400 ft. 1995: On disturbed site (gravel piles).	1970: Reproductive status: flower and fruit. 1995: Plants numerous. Reproductive status: flower and fruit.	1970: Original id: <i>O. caespitosa</i> Nutt. Annotated <i>O. harringtonii</i> ; note <i>Puccinia</i> spp. rust ascospores on leaves, determined by R.A. Raguso, June 14, 2001. 1995: Original id: <i>Pachylophus eximius</i> . Annotated <i>O. harringtonii</i> by W.L. Wagner 1980.
6	June 14, 2000	Plants occupied a small area of road-cut along a gravel road. Plants were seen on the steep, encircling edge of the road-cut and in the depression between the side of the road cut and the road. Aspect: southeast, slope 30 degrees. Moisture: mesic/xeric. Full sun light exposure. Gypsum rich parent material. Surrounded by <i>Frankenia</i> spp. and <i>Oryzopsis</i> species. Associated species: <i>Yucca glauca</i> , <i>Grindelia</i> spp., <i>F. jamesii</i> , <i>O. hymenoides</i> . Elevation 5,587 ft.	Number of individuals: 33 in approximately a 50 m area. 80 percent vegetative, 20 percent with fruit.	No evidence of disease predation or injury.

Arbitrary Occurrence Number	Dates Observed	Habitat	Abundance and reproductive status	Comments
7	May 28, 1954	No information.	No information.	No information.
8	July 2, 1967	Silt with shale soil on sloping road bank.	No information.	No information.
9	June 12, 1942	1942: In dry sandy soil on edges of banks of arroyo and along dissected stream course in full sun.	1942: Several plants. Reproductive status: fruit. Overwintering fruits conspicuous. 1998: Plants not found although the specific area observed in 1942 may not have been found.	1942: Original id: <i>O. caespitosa</i> Nutt. Annotated <i>O. harringtonii</i> by W.L. Wagner 1980.
10	May 26, 1995	On east-facing road cut in Pierre Shale.	Reproductive status: Flower and fruit.	Major taproot; not obvious annual.
11	June 13, 1993; 1995; May 26, 1998	On steep clay road cuts.	1993: Reproductive status: Flower and fruit. 1998: 29 individuals varying in size from a small rosette to a taller plant.	1993: Occasional plants stemless but the great majority leafy. Flowers much smaller than <i>O. caespitosa</i> . 1995: Major taproot, obviously not an annual, stem approximately 6 inches tall. 1998: Stem ranges from 3 to 9 inches in height. In flower, one dead plant with last years fruit observed on the ground.
12	May 27, 1998	Along a dirt road, between the road and a fence. Associated with <i>Allium textile</i> , <i>Sphaeralcea coccinea</i> , <i>Penstemon auriberbis</i> , <i>Oryzopsis hymenoides</i> in clay soils. The surrounding habitat is grazed short grass prairie.	Five individuals, three of which had withering flowers.	<i>Melilotus officinale</i> is encroaching on the plants. Fence or road maintenance may disturb the plants. Herbicide spraying along the road should be avoided.
13	May 28, 1997	With <i>Sophora nuttalliana</i> at 5,400 ft elevation.	Abundant along roadsides especially in old tank tracks.	No information.
14	June 11, 1968	Dry rangeland at 1,798 m (5,900 ft) elevation	No information.	No information.
15	May 19, 1948	No information.	Reproductive status: flower.	Flowers white, withering pink. Original id: <i>O. caespitosa</i> . Annotated <i>O. harringtonii</i> by W.L. Wagner 1980.
16	June 2, 1995	Shale outwash area.	Six individuals. Reproductive status: Flower and fruit.	No information.
17	May 24, 1997	Associated species: <i>Echinocereus reichenbachii</i> , <i>Euphorbia lata</i> , <i>Frankenia jamesii</i> , <i>Hymenoxys acaulis</i> , <i>E. spathulata</i> , <i>Lesquerella fendleri</i> , <i>Penstemon auriberbis</i> , <i>Stanleya pinnata</i> .	14 individuals counted.	No information.
18	June 13, 1891	No information.	No information.	No information.
19	June 12, 1936	No information.	Reproductive status: flower and fruit.	Original id: <i>Anogra violacea</i> . Annotated <i>O. harringtonii</i> by W.L. Wagner 1980.

Arbitrary Occurrence Number	Dates Observed	Habitat	Abundance and reproductive status	Comments
20	May 21, 1995	Shaley slopes with <i>Atriplex</i> sp. and <i>Frankenia</i> sp. on barren areas at elevation 5,100 ft.	No information.	No information.
21	1897; 1900; June 3, 1931	1900: Mesas. 1931: Stony ridges.	No information.	Site is now [2004] likely to be in or near a gravel pit.
22	July 1897, 1908	No information.	1897: Reproductive status: fruit. 1908: Reproductive status: flower and fruit.	Original id: <i>Oenothera</i> ssp. Annotated <i>O. harringtonii</i> by W.L. Wagner 1980.
23	July 17, 2001	Roadside occurrence on outcrop of shale growing with <i>Oonopsis puebloensis</i> .	Estimated population size of 50 individuals. Plants were flowering on May 31, 2001 and fruiting on July 17, 2001.	White flower color.
24	June 3, 1998; May 31, 2001	1998: Within shortgrass prairie. Associated species include: yucca, <i>Frankenia jamesii</i> , <i>Oryzopsis hymenoides</i> , <i>Opuntia</i> sp., <i>Penstemon auriberbis</i> , <i>Oonopsis fremontii</i> , <i>Aristida</i> sp., <i>Hilaria jamesii</i> , <i>Allium textile</i> , <i>Artemisia bigelovii</i> , <i>Lesquerella</i> sp., <i>Oreocarya</i> sp., <i>Leucelene</i> sp., globemallow, blackfoot daisy, winterfat. 50 percent vegetation cover on clay soils with shale or milstone gravel. Elevation 5,440 ft.	1998: 20 plants in flower (seen at 10 a.m.) 2001: One individual observed. Several fruit.	1998: Good size classes. Pressures from urban development are high.
25	July 19, 2001	Shale barren. Along base of steep grey shale outcrop with <i>Mentzelia chrysantha</i> , <i>Atriplex</i> sp., and <i>Eriogonum</i> sp. Base of slope is weedy with <i>Melilotis officinale</i> , <i>M. alba</i> , <i>Bromus</i> sp., <i>Kochia</i> sp., <i>Helianthus</i> sp., gumweed. Aspect 5 degrees, xeric, part shade. Fine textured soil of limestone/shale parent material.	Eight individuals counted. All individuals had fruit.	Plants dried light brown and were approximately 20 cm or more tall. Fruit with stout knobby ridges. Bike path follows the base of the slope.

Table 4. Plant species reported to be associated with *Oenothera harringtonii*. This is not an exhaustive list and represents only the observations that were made on herbarium sheets, in Goeken (1968), by personal observation of the author, and in Colorado Natural Heritage Program (2002).

Associated species	Associated species (continued)
<i>Aegilops cylindrica</i> [non-native]	<i>Lesquerella fendleri</i>
<i>Allium textile</i>	<i>Lesquerella</i> spp.
<i>Aristida</i> spp.	<i>Leucelene ericoides</i>
<i>Artemisia bigelovii</i>	<i>Melampodium leucanthum</i> (reported as black-foot daisy)
<i>Astragalus</i> spp.	<i>Melilotis alba</i> [non-native]
<i>Atriplex confertifolia</i>	<i>Melilotis officinale</i> [non-native]
<i>Atriplex</i> spp.	<i>Mentzelia chrysantha</i>
<i>Bouteloua gracilis</i>	<i>Haplopappus fremontii</i> (reported as <i>Oönosis fremontii</i>)
<i>Bromus tectorum</i> [non-native]	<i>Oönosis puebloensis</i>
<i>Bromus</i> spp.	<i>Opuntia</i> spp.
<i>Convolvulus arvensis</i> [non-native]	<i>Oreocarya</i> spp.
<i>Echinocereus reichenbachii</i>	<i>Oryzopsis hymenoides</i>
<i>Eriogonum</i> spp.	<i>Penstemon auriberbis</i>
<i>Euphorbia lata</i>	<i>Penstemon</i> spp.
<i>Euphorbia spathulata</i>	<i>Psoralea tenuiflora</i>
<i>Eurotia lanata</i> (reported as winterfat)	<i>Sacobatus vermiculatus</i>
<i>Frankenia jamesii</i>	<i>Salsola tragus</i>
<i>Gaura coccinea</i>	<i>Sophora nuttalliana</i>
Grasses (unidentified)	<i>Sphaeralcea coccinea</i>
<i>Grindelia squarrosa</i>	<i>Sphaeralcea</i> spp. (reported as globemallow)
<i>Grindelia</i> spp. (reported as gumweed)	<i>Sporobolus asper</i>
<i>Gutierrezia sarothrae</i>	<i>Sporobolus cryptandrus</i>
<i>Helianthus</i> spp.	<i>Stanleya pinnata</i>
<i>Hilaria jamesii</i>	<i>Stipa commata</i>
<i>Hymenoxys acaulis</i>	<i>Yucca</i> spp.
<i>Kochia scoparia</i> [non-native]	<i>Yucca glauca</i>
<i>Lepidium</i> spp.	

barren areas they are reported to extend into densely weedy areas. Conversely, these observations may indicate that the weeds are encroaching on barren habitat that was initially colonized by the *Oenothera*. The latter case is most likely. Weeds observed to be threatening stands of *O. harringtonii* include tansymustard (*Descurainia* spp.), Russian thistle (*Salsola* spp.), sweetclover (*Melilotis officinalis*), field bindweed (*Convolvulus arvensis*), wild rye (*Elymus elymoides*), cheatgrass (*Bromus tectorum*), Mexican-fireweed (*Kochia scoparia*), jointed goatgrass (*Aegilops cylindrica*), and pepperweed (*Lepidium* spp.).

Reproductive biology and autecology

Oenothera harringtonii flowers from mid-May through June, and its fruits mature in July. The flowers are white-colored, relatively small (approximately 4 cm in diameter), and strongly scented, the perfume reminiscent of gardenia flowers (Goeken 1968, Wagner et al. 1985). The stigmas and anthers are spatially separated within flowers, but the distance separating them (floral herkogamy) varies considerably among populations of *O. harringtonii* (Raguso personal communication 2003). Herkogamy, the spatial

separation of anthers and stigmas (male and female reproductive organs), is understood to have evolved to ensure outbreeding. The distance between the anthers and stigmas influences which organisms are effective pollinators. Organisms that are significantly smaller than the distance between the anthers and stigmas will be able to “steal” pollen without performing any pollination service. Anthers and stigmas are usually separated by approximately 1 cm in most populations of species in the *O. caespitosa* complex (Raguso personal communication 2003). *Oenothera harringtonii* plants in the Pueblo and Florence populations are unusual in that their flowers do not show substantial herkogamy and the anthers and stigmas can be the same length (Raguso personal communication 2003).

A particularly high number of flowers (five to 10) per stem open each day. Studies have shown that large white or yellow flowers of *Oenothera* species generally open just before or after sunset and are pollinated by hawkmoths while the smaller, usually yellow, flowers of other *Oenothera* species open in the early morning and are generally pollinated by bees (Gregory 1964b). This observation is consistent with that of Wagner et al. (1995), who described all members of *Pachylophus* to have flowers that open after sunset and fade in the morning sun. However, some species appear to have variations to this syndrome. During studies on populations of *O. caespitosa* ssp. *montana* and ssp. *marginata* in California, it was observed that even though their flowers were open in the evening and through the night, they remained open for part of the following morning (Linsley et al. 1963). This crepuscular-nocturnal-morning habit is likely true for flowers of *O. harringtonii* whose flowers have been observed to be open at dusk, dawn, and in the morning to at least just after 10 a.m. and possibly later (Colorado Natural Heritage Program 2002, Raguso personal communication 2003, Spackman Panjabi 2004, author’s personal observation 2003).

Oenothera harringtonii is self-incompatible and an obligate outcrosser (Stockhouse 1973). Russell and Levin (1988) compared closely related *Oenothera* species having different breeding systems and found that obligate outcrossers were competitively superior to facultatively selfing taxa, whose progeny were identical to the parent. The self-incompatibility system operating within the Onagraceae is gametophytic, involving a series of S-alleles (Raven 1979). In this type of system, pollen tube growth is initiated, but the tube stops growing in the style (Stanley and Linskens 1974).

Oenothera harringtonii is a diploid species with a gametophytic chromosome number of 7 ($2n = 14$, Goeken 1968). Controlled hybridization experiments between *O. harringtonii* and other members of the *O. caespitosa* complex demonstrated that hybrids are easily produced (Goeken 1968, Stockhouse 1973, Wagner et al. 1995). Hybrids between *O. harringtonii*, *O. caespitosa* ssp. *macroglottis*, and *O. caespitosa* ssp. *marginata* showed a high degree of genome homology by producing seven bivalents at Metaphase I of meiosis. This indicates a close relationship between the three species (Goeken 1968). Goeken (1968) concluded that *O. harringtonii* is a xeric derivative of *O. caespitosa* ssp. *macroglottis*. Hybrids between these species have not been reported in nature. Several barriers to gene exchange between two sympatric species may exist. There may be differences in the assemblage of pollinator species that are a result of either temporal isolation or mechanical isolation. For example, the temporal difference in the flowering period reduces the hybridization potential of two southwestern *Oenothera* species that grow together but are pollinated by different species of solitary bees that forage at different times (Raven 1962). Mechanical isolation is a result of different structural characteristics of the flower that permit only dissimilar species to effect pollen transfer (Grant 1981).

Oenothera harringtonii is an annual or biennial species (Wagner et al. 1985, Kelso personal communication 2003, Raguso personal communication 2003). In greenhouse situations, under well-watered and fertilized conditions, *O. harringtonii* plants always bloom within the first few months of germination (Raguso personal communication 2003). However, environmental variation in microsites might result in plants becoming facultative biennials, or simply not blooming at all (Raguso personal communication 2003). From observations on garden-grown plants, *O. harringtonii* has also been reported to be a short-lived perennial (Weber and Wittmann 2001, Wittmann personal communication 2003).

A biennial is defined as a plant that lives for two years (Allaby 1992). It is vegetative during the first year and reproduces and dies during the second year. A perennial plant, on the other hand, normally lives for more than two seasons and, after the initial vegetative period, produces flowers annually (Allaby 1992). However, it is doubtful that this strict horticultural understanding of the biennial habit is so clearly defined in nature (Harper 1977). Some biennials remain vegetative for several

years when the environment is unfavorable while others flower within a year under favorable conditions (Hirose and Kachi 1982). A critical feature of the biennial habit is that plants die after flowering, although in the case of many biennial species, death does not automatically follow flowering *per se* and life may be prolonged if the inflorescence is destroyed, for example by herbivores, before seed set (Harper 1977). Harper suggests that this type of biennial be described as a perennial monocarpic species with the potential for completing their life cycle within two years. If a plant flowers in consecutive years but declines in vigor after the first year of flowering, it should be called a short-lived perennial.

Although the evidence indicates that *Oenothera harringtonii* is predominantly annual or biennial in natural habitats, further studies are warranted to determine the extent of the range of growth habitat that it can exhibit. It is notable that perennialism is the ancestral state for its lineage, and that *O. harringtonii* is more derivative in many respects, including its gardenia-like fragrance and its smaller and more numerous flowers, than some other members of the *O. caespitosa* group (Raguso personal communication 2003).

Oenothera harringtonii plants produce approximately six to 20 capsules per stem and 60 to 100 seeds per capsule (Wagner et al. 1985). Seed production tends to be more abundant than in other members of the *O. caespitosa* complex. Wagner et al. (1985) suggested that this was a result of its annual growth habit. The abundance of seed does suggest that there is a very high degree of seedling mortality and/or a requirement for a large seed bank in the soil.

The mechanism of capsule dehiscence depends upon species and has not been documented for *Oenothera harringtonii*. It may be one of three types: hygrochasy, xerochasy, or tachyspory. Many members of the genus *Oenothera* have hygrochastic capsules, that is, capsules that open when moist (Poppendieck 1995). Hygrochasy is a relatively rare phenomenon but is surprisingly common within the *Oenothera* genus and is correlated with the expansion of species into both particularly xeric and hydric habitats. In xeric habitats, rain will prompt dehiscence and raindrops will contribute to seed dispersal (Poppendieck 1995). The more familiar xerochasy, where dry conditions promote capsule dehiscence and moist conditions cause closure, is also found within the genus, specifically within the *Megapterium* section (Poppendieck 1995). A third type of dehiscence (tachyspory) is that which always occurs upon maturation as part of the ripening process (Poppendieck 1995).

The capsules of the majority of the species in the *Oenothera caespitosa* complex only dehisce along part of their length, and the seeds that are retained often become buried with the capsules (Wagner et al. 1985). The capsules, which eventually deteriorate and release the seeds, can often remain on the mother plant for an extended period of time or accumulate at its base. In both cases seed dispersal is very localized. After the capsule has split, seeds may be dispersed in several ways (see Community ecology section). It is likely that seeds remain viable for a long time in the seed bank. A generalization is that species that grown in disturbed environments and have small-sized seeds tend to have long-lived seeds (Harper 1977, Fenner 1992). Beal's long-term experiments at Michigan State University, where seeds and soil were placed in pint bottles and buried in 1879, demonstrated that seeds of *O. biennis* could remain viable after being buried for 50 years (Zeevaert personal communication 1981). A persistent seed bank is also consistent with the model of a species whose habitats are subjected to temporally unpredictable disturbance and environmental conditions, such as flash floods and drought (Grime et al. 1988, Pake and Venable 1996). Seed longevity has been proposed as a viable life strategy alternative to long-distance seed dispersal (Harper and White 1974).

Oenothera harringtonii has been cultivated in several gardens (Kelso personal communication 2003, Wittmann personal communication 2003). The seed appears to germinate without any treatment prior to planting (Wittmann personal communication 2003). In contrast, some seeds required "nicking with a razor blade" (scarification) in order to germinate in petri dishes (Stockhouse personal communication 2003). Transplanting adults has been reported to be generally unsuccessful (Goeken 1968, Stockhouse personal communication 2003). In addition, seeds taken from the transplants failed to germinate (Goeken 1968). However, the seed in this case may have been immature; viable seed has been found when the capsules are collected well before dehiscence (Wittmann personal communication 2003).

Demography

Oenothera harringtonii only reproduces sexually (Wagner et al. 1985). No demographic studies have been undertaken, and transition probabilities between the different stages, from seed production to the flowering adult, are unknown. Many biennials have a critical plant size for flowering (Gross 1981, Hirose and Kachi 1982). Werner and Caswell (1977) demonstrated that the population growth of the biennial, *Dipsacus*,

was explained more satisfactorily on a model based on size rather than age. Gross (1981) showed that the size of the rosette of *O. biennis* was directly related to the probability of its flowering and directly but negatively related to the probability of its death. That is, all individuals had to reach a minimum rosette diameter before flowering, and the smallest rosettes had the highest probability of dying. She observed that proportionally more small-sized than large-sized rosettes died, and no rosettes that reached 14.5 cm or more in diameter died before flowering. In addition to a critical size, many biennials need to experience specific environmental conditions before flowering (Hirose and Kachi 1982). For example, *O. erythrosepala* has vernalization requirements. Even if it has reached the critical size for flowering, it will not flower unless it experiences adequately low temperatures (vernalization) during the winter (Hirose and Kachi 1982). It has been proposed that a critical size is necessary in order for the plant to produce a high number of well-filled seeds (Hirose and Kachi 1982). At one *O. harringtonii* population studied by Goeken (1968), plants were described as overwintering as rosettes and flowering in the spring, but the mortality rate was not noted. Fall germination after late summer rains is not unusual among species of *Oenothera* (Harper 1977).

Occurrence sizes of *Oenothera harringtonii* are typically small. When surveys have been made, typically between May and the end of July, populations often appear to be largely composed of reproductive adults. This is expected for a biennial species that germinates during the mid to late summer rains, overwinters as a rosette, and flowers the following spring. However, small rosettes have also been observed at some occurrences during the same time of year. For example, 80 percent of the individuals were described as vegetative in June (**Table 2** and **Table 3**; Colorado Natural Heritage Program 2002). It is unlikely that small rosettes would flower in the current year. This is similar to the population structure observed in May 2003 where 70 plants were counted (author's personal observation 2003). At this population, there were 28 flowering individuals and 42 vegetative rosettes with leaf lengths between 2.5 and 7 cm.

Field observations suggest that *Oenothera harringtonii* populations are particularly ephemeral in nature (Kelso personal communication 2003, Raguso personal communication 2003). *Oenothera harringtonii* plants appear to be exceptionally abundant in some years and exceedingly scarce in others. Unlike most perennial *Oenothera* species, it is often difficult to find extant plants in the places where others have been collected

in previous years (Kelso personal communication 2003, Raguso personal communication 2003). Although seed production and germination are noted to be high during wet years, the ephemeral nature of populations is not necessarily related to environmental conditions. A large population of both rosettes and flowering plants one year may disappear the following year even though the conditions appear to be about the same during the consecutive years (Kelso personal communication 2003). After a population has been observed, revisiting the same site over many consecutive years would be very valuable in understanding the dynamics and structure of the population.

Population viability analyses for this species have not been undertaken. The relatively few individuals at each site and the predominance of adults (flowering individuals) raise questions as to the germination rate of the apparently large number of seeds that are produced (Wagner et al. 1995). Even though high numbers may be lost to predation (Harper and White 1974), it is somewhat hard to reconcile the small occurrence sizes with the high number of seeds produced. It may be that small rosettes go unnoticed and the seedling mortality rate is high. Alternatively, seed recruitment may be periodic in nature, and a high number of seedlings only occurs in some years. The observation that there are years when *Oenothera harringtonii* plants are very abundant or very scarce supports the latter hypothesis. There is also comparative evidence within the genus *Oenothera* that supports the former hypothesis. *Oenothera avita* ssp. *eurekaensis* is a short-lived perennial species endemic to the semi-stabilized sand dunes of Inyo County, California. Pavlik and Barbour (1988) reported that most individual plants had a high mortality and a relatively short lifespan, but these disadvantages were offset by copious seed production, long-lived seeds, low to moderate seed predation, and frequent establishment. In fact both patterns appear to agree with what is known about *O. harringtonii*, and it may be that a combination of the two strategies is exhibited. The seed scarification requirement observed during *in vitro* germination studies suggests that a physical dormancy is imposed on seeds, contributing to their longevity in the soil (see Reproductive biology and autecology section).

Limits to population growth are not well defined. Appropriate soils and soil structure may influence the establishment of flowering individuals. In addition, recent work suggests that interactions between plants and soil microbes are important (Callaway and Ascheloug 2000, Olff et al. 2000). Klironomos (2002) demonstrated that the interaction between

certain soil microbes and different plant species explained a significant proportion of the variance in the relative abundance of rare and invasive species in plant communities in an old-field habitat. Some plant species accumulate pathogens quickly and maintain low densities as a result of the accumulation of species-specific pathogens, which he termed “negative feedback” (Klironomos 2002). An example that may be relevant to *Oenothera harringtonii* was that *O. biennis* was found to have a negative feedback and was also found to have relatively low abundance in an old-field habitat (Klironomos 2002). Local micro-environmental

habitat conditions may also be important. Although disturbance may be necessary for seed germination, too frequent or too high levels of disturbance will likely negatively impact populations over the long term.

A simple lifecycle model for *Oenothera harringtonii* is described in diagrammatic terms (**Figure 5**). The proposed model is based on *O. harringtonii* being either annual or biennial, but the same scheme may also apply to a monocarpic (semelparous) perennial. Size may be important in determining which of the plants flower, either during

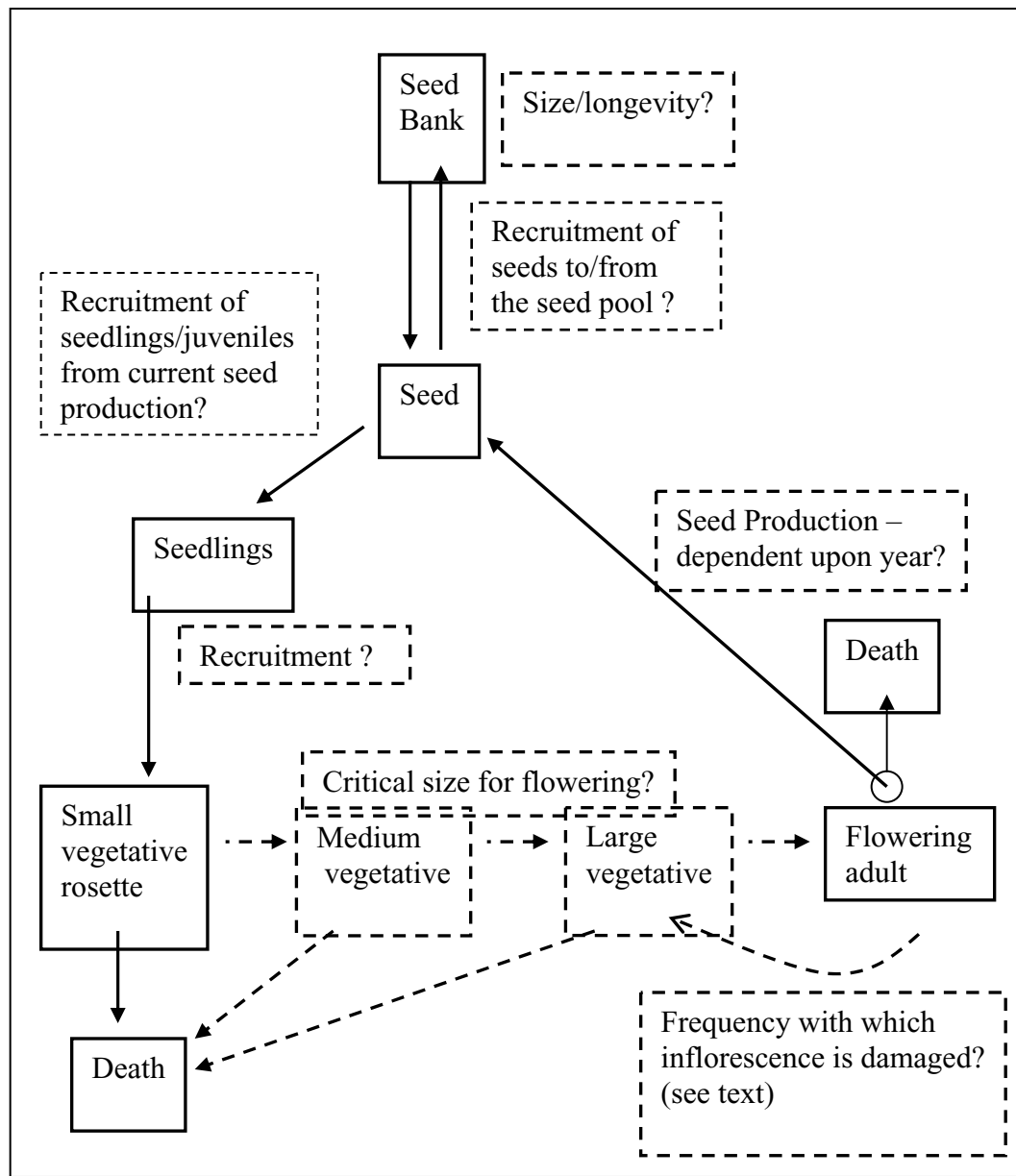


Figure 5. Proposed lifecycle diagram for *Oenothera harringtonii*.

the first (annual) or second (biennial) year. Heavy arrows indicate phases in the life cycle that are known, and lighter weight arrows indicate the phases that need clarification. The steps that particularly need to be clarified are noted by “?” at the appropriate arrow. More information is needed to define which of the life history stages have the greatest effect on population growth and survival. Specifics on population projection analyses are unavailable, but some generalizations may be made from comparative species investigated by Silvertown et al. (1993). However, it is emphasized that these are generalizations, and Silvertown et al. (1993) demonstrated that there were several exceptions to the general rules. Although seedling recruitment was particularly important to certain short-lived semelparous perennial forbs, progression from one stage to another was more important than seed or seedling recruitment for most forb species. That is, growth and fecundity are more important than stasis (Silvertown et al. 1993). In addition, *O. harringtonii* appears to be strongly dependent on seedling recruitment for population growth because there appears to be no clonal (ramet) reproduction.

Characteristics of the life cycle and habitat of *Oenothera harringtonii* make it somewhat difficult to classify with respect to its ecological strategy. It appears to be appropriate to characterize it as an r-selected species as outlined by MacArthur and Wilson (1967). This is a species that has evolved in an environment with no crowding and harvests the most food to produce the largest number of offspring. Extending this concept, Grime et al. (1988) suggested that species could be placed in one of seven life strategy categories. *Oenothera harringtonii* is apparently annual or biennial and produces high numbers of seed. However, it is unclear if the offspring are capable of a long-term persistence in the juvenile state in some circumstances or if there is always high seedling mortality. Whatever the situation, relatively few flowering individuals are found at one time. Thus, although *O. harringtonii* has many of the characteristics of a ruderal species, it also appears to have some features that support it being stress tolerant. Therefore it is appropriately given the somewhat conflicting designation of a “stress-tolerant ruderal” strategist.

Community ecology

Oenothera harringtonii is self-incompatible and relies on pollinators for cross-pollination (see Reproductive biology and autecology section). At the time of anther dehiscence, *Oenothera* pollen is bound in a sticky viscid threadlike mass that makes it easily

transportable by visiting insects (Stanley and Linskens 1973). The pollination biology of the *Oenothera* genus has been studied quite extensively.

Gregory (1964a, 1964b) reported an extensive study on hawkmoth pollination among *Oenothera* species. He primarily studied *O. hookeri* (sub-genus *Oenothera*) but also reported on pollinators of *O. caespitosa*. He observed that several species of hawkmoths (five species of *Sphinx*, *Celerio lineata*, and *Manduca quinquemaculata*) and bees of two genera (*Lasioglossum* spp. and *Agapostemon* spp.) visit *O. caespitosa*. Species of sphinx moth, *M. quinquemaculata*, and the nocturnal bee *L. (Sphecodagastra) texanum* were also observed visiting *O. caespitosa* ssp. *macroglottis* in Colorado (Stockhouse 1973, Wagner et al. 1985). Bees (*L. sisymbrii*, *L. trizonatum*, and *Adrena anograe knowltoni*) were observed collecting pollen from *O. caespitosa* ssp. *macroglottis* in the early morning (Stockhouse 1973, Wagner et al. 1985). However, several bee species, including members of the Halictidae family such as *Lasioglossum* species, and of the Apidae family such as *Sinhalonia* “longhorn” bees, strip stamens of pollen but typically do not contribute to pollination because of floral herkogamy (Ragusa personal communication 2003).

Limited pollination studies have been carried out specifically on *Oenothera harringtonii* (Stockhouse 1973, Spackman Panjabi 2004, Ragusa personal communication 2003). Observations made on *O. harringtonii* plants indicate that the white-lined sphinx moth (*Hyles lineata*) is a significant pollinator species (Spackman Panjabi 2004, Ragusa personal communication 2003). Bees also appear to be important pollinators of *O. harringtonii* (Spackman Panjabi 2004). Even though some bee species, for example *Lasioglossum* species of the Halictidae family, may not be effective pollinators in all populations, because of the variation in herkogamy among *O. harringtonii* populations most bee visitors are likely to function as pollinators at the populations where the flowers possess anthers and stigmas of similar length, for example around Pueblo and Florence (see Reproductive biology and autecology section). Arthropods with variable pollination effectiveness are termed conditional pollinators (Ragusa personal communication 2003).

During a pollination biology study in early June 2003, arthropods were collected from *Oenothera harringtonii* plants at two sites, one in Pueblo County and the other in Huerfano County, over a total of 4.5 hours (Spackman Panjabi 2004). Of the seven arthropod species collected and identified, six were bees in the

order Hymenoptera and only one was a hawkmoth, *Hyles lineata* (Spackman Panjabi 2004). Bees of four genera, Andrenid bees (*Andrena* spp.), halictid bees (*Lasioglossum sedi* and *Agapostemon texanus*), and carpenter bees (*Anthophora portera*), were among those collected (Spackman Panjabi 2004). Apparently, *Adrena anograe knowltoni* collects pollen from species of *Oenothera* species with large white flowers rather than the yellow-flowered species even though it will also visit *Stanleya pinnata* (Linsley et al. 1963). *A. anograe knowltoni* is thus likely to be among the *Adrena* species visiting *O. harringtonii*. During the same 2003 study, nine additional 30-minute visual observations of insect visitation on *O. harringtonii* flowers were made (Spackman Panjabi 2004). Observers were able to distinguish between flies, bees, beetles, and sphinx moths. A total of 42 insect visits were recorded during the course of all nine 30-minute observations. Of the 42 visits, 33 (79 percent) were by sphinx moths (*Hyles lineata*), six (14 percent) were by bees, two (5 percent) were by flies, and one (2 percent) was by a beetle (Spackman Panjabi 2004). The total average visitation rate for all of the insects that visited *O. harringtonii*, including sphinx moths, flies, bees, and beetles, was 0.89 visits per open corolla per 30 minutes (Spackman Panjabi 2004). Bumblebees were noted to visit outside the observation periods (Spackman Panjabi 2004).

In the absence of direct pollination studies, comparing known characteristics of one plant species with those of other species in the same genus that have been examined in more detail can provide a more comprehensive understanding of its pollination strategy. The flowers of *Oenothera harringtonii* appear to more closely resemble the flowers of *O. psammophila* than those of the sympatric species *O. caespitosa* ssp. *macroglottis*. *Oenothera psammophila* is an eco-geographically isolated, but genetically related, species occurring in Idaho (Stockhouse 1973). The flowers of both *O. harringtonii* and *O. psammophila* have a nearly vertical platform and therefore appear to be better adapted to smaller hawkmoths and to bees (Stockhouse 1973, Wagner et al. 1985). The behavior of the hawkmoths visiting *O. caespitosa* ssp. *macroglottis* was fairly consistent (Stockhouse 1973, Wagner et al. 1985). They hovered, inserted their proboscis, and then landed on the wide, nearly horizontal platform of petals (Stockhouse 1973, Wagner et al. 1985). In contrast, *Hyles* species are relatively small hawkmoths that hover rather than land on the corolla to get nectar, so they also transfer less pollen at one time than their larger relatives.

Pollinator behavior has been studied over three *Oenothera caespitosa* ssp. *macroglottis* populations and one *O. psammophila* population (Stockhouse 1973). The *O. caespitosa* ssp. *macroglottis* populations, each with between 75 and 100 individuals, were separated by one and seven miles respectively. Pollination studies that involved dusting the flowers with different colored dust showed that *O. caespitosa* ssp. *macroglottis* pollinators frequently made flights of eight and nine miles and that several moths had flown at least 20 miles within a period of three successive nights (Stockhouse 1973). This supports Gregory (1964b) who suggested that individual hawkmoths could travel over large areas and were responsible for the widespread cross-pollinations he observed among *Oenothera* plants. The pollinators and the extensive distances traveled within *O. caespitosa* ssp. *macroglottis* populations were dissimilar to the patterns observed among the *O. psammophila* population. In this case, no *Sphinx* or *Manduca* species, only *Hyles* hawkmoth species, were observed. Additional pollinators of *O. psammophila* were Halictid bees and noctuid moths (Stockhouse 1973). Using the same method of detecting colored dust, Stockhouse (1973) concluded that unlike *O. caespitosa* ssp. *macroglottis*, negligible inter-population pollen dispersal was occurring. However, the reasons for this are unclear. Ostensibly it would appear that pollinator behavior may be responsible, but the plant population sizes were also different. The population size of *O. psammophila* was at least double that of *O. caespitosa* ssp. *macroglottis*; from 200 to 500 individuals versus 75 to 100 individuals (Stockhouse 1973).

The similarity of the pollinators observed between *Oenothera harringtonii* and *O. psammophila* suggests that the pollinator behavior (short-distance pollination activity) may also be similar. However, it may be that some degree of extensive long-range cross-pollination activity can be expected in the case of *O. harringtonii* since it shares the characteristic of small population size with *O. caespitosa* ssp. *macroglottis*. In addition bumblebees, which tend to forage over long distances, were observed visiting some *O. harringtonii* flowers (Spackman Panjabi 2004). Osborne et al. (1999) tracked individual bumblebees using harmonic radar and recorded that most bees regularly fly over 200 m (range 70 to 631 m) from the nest to forage even when apparently plentiful food was available nearby. Pollinator behavior characteristics suggest that long-distance pollen load transfer may be small. However, although there is precedence for a critical pollen load on the stigma before effective pollination can occur,

potentially it may require little pollen transfer to affect cross-pollination. While long-range cross-pollination may be infrequent, exchange of genetic material is potentially possible between quite widely spaced occurrences (see Definitions section for authorities of pollinator species mentioned in this section).

The typical small population size of *Oenothera harringtonii* suggests that they would not be particularly rewarding, and therefore attractive, to arthropod visitors relative to any alternative large stands of densely growing flowers. However, the comparatively high number of flowers per stem and large nectar reward may compensate to some extent for the relatively few individuals. In a study on one *O. harringtonii* population, it was measured that each flower produced between 5 to 32 μ l (average of 20 μ l) of nectar, of which 35 percent was sucrose. Other sugars include glucose, fructose, and an unknown (Stockhouse 1973). Thus there is approximately 200 μ l of nectar and 70 μ l of sucrose available per plant, which represents a significant energy resource.

There is evidence of arthropod predation. *Hyles lineata* female moths are predators as well as pollinators (Raguso personal communication 2003, Spackman Panjabi 2004). *Hyles lineata* moths lay eggs on *Oenothera harringtonii* plants, and their hornworm larvae eat the buds, flowers, and new leaves (Raguso personal communication 2003). A very small moth, *Mompha* spp., has also been observed to lay eggs in *O. harringtonii* flowers, and the larvae eat the ovules and developing seeds, much like the yucca moth (*Tegeticula maculata*) (Raguso personal communication 2003). It is unlikely that the *Mompha* moths play any role as pollinators, but they certainly impact reproduction (Raguso personal communication 2003). However, seed predation by arthropods is not necessarily bad at levels under which the species has evolved and may be important to long-term species sustainability. In some cases, for example, within the genus *Astragalus*, this predation may have had an important influence on population dynamics and diversity (Green and Palmbald 1975, Mancuso and Moseley 1993).

There is very little information on microbial associations with *Oenothera harringtonii*. Arbuscular mycorrhizal fungi are beneficial soil microbial organisms and are likely to be associated with *O. harringtonii* since they have been found to colonize other *Oenothera* species (Klironomos 1998, Klironomos 2003). These fungi are often important for efficient nutrient uptake in poor soils. Ascospores of the pathogenic fungi, *Puccinia* or rust, have been

associated with leaf tissue (Occurrence 5, [Table 1](#)). The significance of this observation to the overall health of the population cannot be assessed without further information on abundance and infection frequency.

Observations on the seed dispersal mechanisms specific to *Oenothera harringtonii* have not been made, but by comparison with other species, there are essentially three potential methods. Seeds and capsules may be washed away from the parent plant by rainwater in a process called ombrohydrochory (Poppendieck 1995). Afternoon thunderstorms are frequent in *O. harringtonii* habitat, and seeds and capsules could be washed relatively large distances either in arroyos or by sheet flooding. Wagner et al. (1995) suggested that this might be a particularly good method of dispersal because the seed collar (see non-technical description earlier in this report) provides a good flotation device before they fill with water after a day or so in wet conditions. Dispersal by ants, myrmecochory, is also an effective method for some species of *Oenothera*, which include *O. caespitosa* ssp. *navajoensis* (Harper 1977, Wagner et al. 1995). Harvester ants (Myrmecinae) gather seeds and store them in underground chambers. Apparently, harvesting activity by ants is not a random process but is species-targeted. Trevis (1958) demonstrated in a desert study that even though the majority of available seed were of a *Plantago* species, 90 percent of the seeds collected by ants were from species in the genera *Oenothera*, *Mentzelia*, and *Malvastrum*. Wagner et al. (1995) reported that rodents might also be involved in seed dispersal. They observed that rodents carried away capsules of both *O. caespitosa* ssp. *macroglottis* and *O. caespitosa* ssp. *marginata* and hypothesized that some seeds would remain uneaten because of the very tough texture of the capsule coat.

An envirogram is a graphic representation of the components that influence the condition of a species and reflects its chance of reproduction and survival. Envirograms have been used especially to describe the conditions of animals (Andrewartha and Birch 1984) but may also be applied to describe the condition of plant species. Those components that directly impact *Oenothera harringtonii* make up the centrum, and the indirectly acting components comprise the web ([Figure 6](#) and [Figure 7](#)). Envirograms are especially useful in formulating hypotheses regarding important links between a species and its environment and therefore can be used to highlight research needs. Much of the information needed to make a comprehensive envirogram for *O. harringtonii* is unavailable. The envirogram in [Figure 6](#) is constructed to outline some of the major components known to directly impact

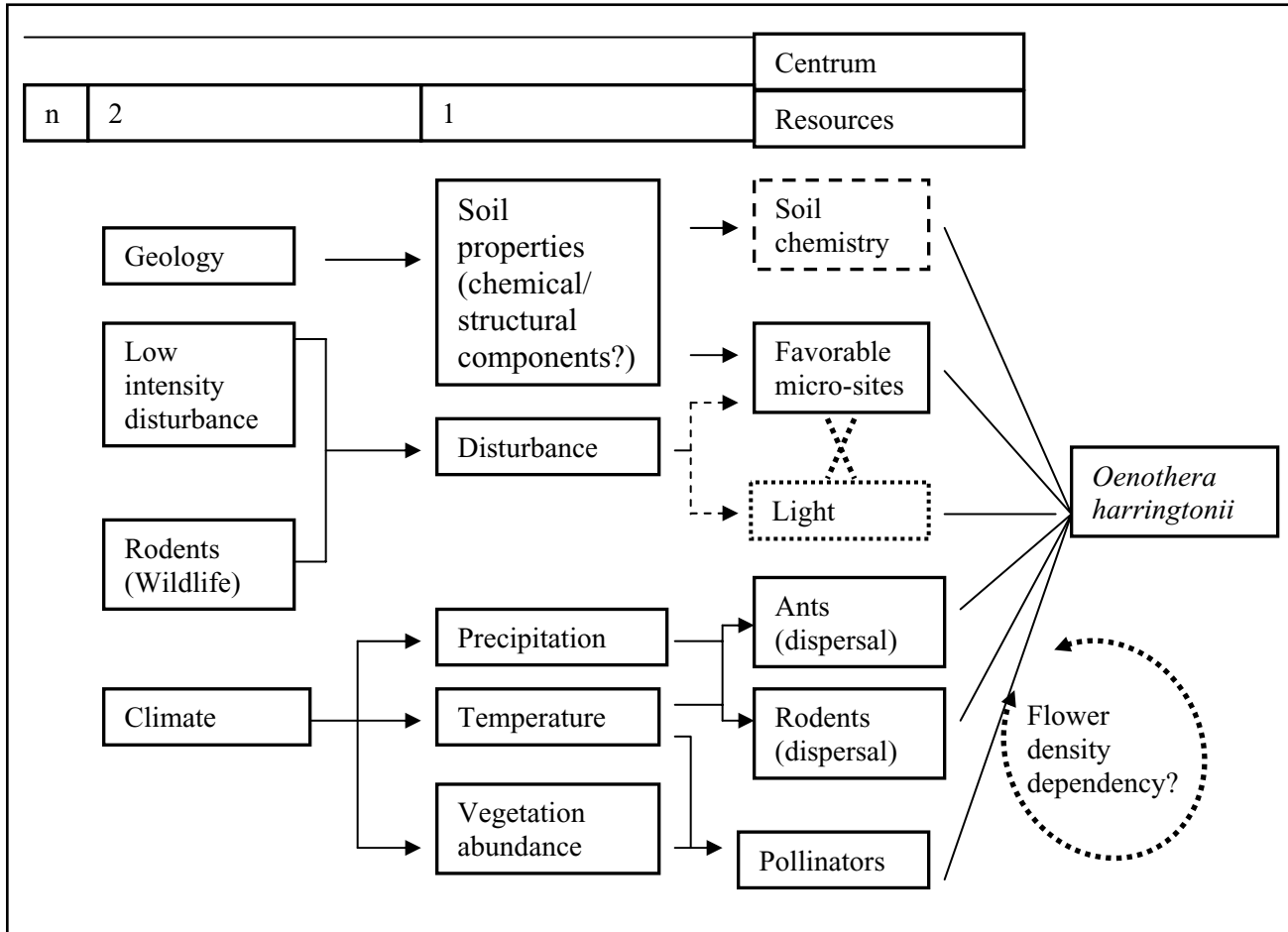


Figure 6. Envirogram of the resources of *Oenothera harringtonii*. The dotted lines indicate that the connections are speculative. The arrowed circle at the pollinator resource suggests that there may be an interaction and pollinator reliability may depend on flower density.

the species. Dotted boxes indicate resources that are of a speculative nature. There is a lack of direct studies on this species that leads to the stretching of the significance of observations and the forming of opinions from inference rather than fact. Inferences need to be tested and should only be applied cautiously when making management decisions.

Resources have been listed as clay soils that provide a suitable edaphic environment and some undefined level of disturbance that will generate microsites for establishment. *Oenothera harringtonii* may not have very stringent growth requirements as it has been described as being easy to cultivate, but it appears to have some specific, if not fully understood, edaphic requirements (Stockhouse personal communication 2003, Wittmann personal communication 2003). Pollinators for cross-pollination are very important as this is a self-incompatible species and arthropods, principally ants, have been suggested as having a role in

seed dispersal. All components of climate, most easily separated into temperature and precipitation, influence this species' growth and development.

CONSERVATION

Threats

The small geographic range of *Oenothera harringtonii* makes it vulnerable to large-scale natural and human-induced disturbances. An additional aspect to its vulnerability is that it is not evenly distributed within its narrow range. Thus, a relatively large proportion of its total population may be susceptible to relatively localized disturbances, such as a large gravel pit.

Habitat loss due to urbanization, mineral and energy resource extraction activities, and road

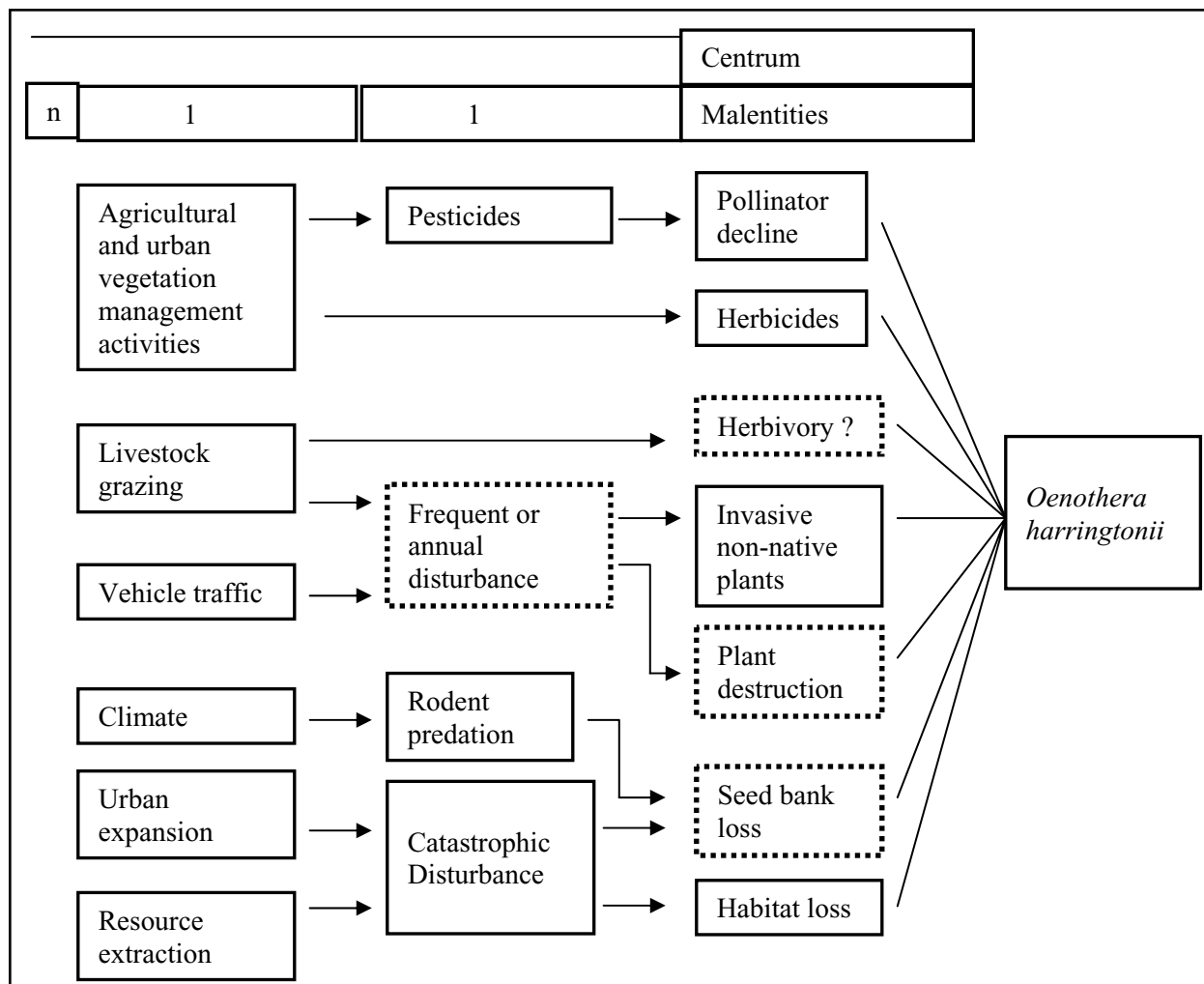


Figure 7. Envirogram outlining the malentities and threats to *Oenothera harringtonii*. The dotted lines indicate that the connections are speculative.

development is a substantial threat to this species (Carsey 1996). The extent of urban development can be equated with population growth. In 1849, when *Oenothera harringtonii* was first collected, the whole state of Colorado had a human population of approximately 34,000 people (US Bureau of the Census undated). In the year 2000, the county of El Paso alone had 516,929 people (U.S. Census Bureau 2001). All of the counties in which *O. harringtonii* occurs have experienced significant increases in human population and associated land use conversion in the last decade. For example, Fremont County experienced a 43 percent increase in human population between 1990 and 2000, and El Paso County experienced a 30.2 percent increase over the same time period (U.S. Census Bureau 2001).

The impacts of resource extraction are difficult to assess since considerable development has been occurring in the area since the mid-1800s, about the

time when *Oenothera harringtonii* was first collected. The area around Florence and Cañon City was one of the earliest sections of Colorado to be developed, the first settlement being in 1840 (Denver & Rio Grande Western Railroad 1936). At that time, considerable land was converted to farmland, and limestone quarries, coal mines, and oil wells were soon to follow. There is evidence that thousands of acres have been disturbed by such activities over more than a century. The City of Portland in Fremont County was particularly noted “because of its thousands of acres of limestone which are used in the manufacture of cement” (Denver & Rio Grande Western Railroad 1936). The Colorado Portland Cement plant has been in operation since 1899. It appears that there continues to be a high degree of limestone use at the present time (Colorado Division of Mining and Geology 2003). At least six known occurrences of *O. harringtonii* are within 6 miles of Portland (Occurrences 6 through 9 [Table 1](#)).

Other sources of disturbance within the occupied habitat of *Oenothera harringtonii* are numerous and include fence, power line, and roadside maintenance; bike riding and other recreational activities; livestock grazing; and fire. The contribution of fire as an agent of natural disturbance may not be particularly significant. Although grassland fires in the shortgrass steppe ecosystem are likely to have occurred at five to ten year intervals (Joern and Keeler 1995), the barren habitats colonized by *O. harringtonii* are unlikely to accumulate sufficient litter to burn so frequently.

Because *Oenothera harringtonii* grows in disturbed areas, such as road cuts, tire tracks, fence lines, highway rights-of-way, and eroding slopes, some level of disturbance appears likely to prompt seed germination and may be important in maintaining populations. However, an interesting fact is that some species that depend upon disturbed habitats are actually eliminated if the disturbance is annual. Three perennial monocarpic species with the potential for a biennial life cycle, namely *Digitalis purpurea* (foxglove), *Dipsacus fullonum* (teasel), and *Daucus carota* (wild carrot), have been studied in detail (Harper 1977). These species possess small seeds, and the seedlings require full light for early establishment into rosettes. These aspects of their life cycle and seed size appear to be comparable to *O. harringtonii*. Although these species may be excluded from late phases of succession, they are also excluded from horticultural and agricultural systems because of the frequency of cultivation (Harper 1977). Although fence and roadside maintenance activities need to be performed, fence lines and highway rights-of-way often provide relatively stable habitats as they are seldom plowed, grazed by livestock, or subjected to intense foot or vehicular traffic. In addition, where soil type prevents a high vegetative cover, the level of maintenance may be low and infrequent. There are numerous examples where populations of rare plants are of particularly high quality along fence lines and associated with the highway right-of-way (Ladyman 2000). Smaller levels of disturbance, such as that provided by rodents and ants and the shrink and swell nature of its typical clay substrate, might be particularly important to population sustainability.

Weed (non-native plant species) proliferation is often a consequence of anthropogenic disturbance, and it may be a substantial threat to *Oenothera harringtonii* habitat. There is relatively little vegetative cover in its natural shale and gravel habitat, and thus *O. harringtonii* is unlikely to be competitive. At least 6 of the element occurrences reported within the last decade (Occurrences 4, 6, 10, 11, 12, and 25, **Table 1**) have

weed infestations. Persistent species that have been used for re-vegetation projects, such as *Melilotis* spp. and *Kochia scoparia*, appear to pose the greatest immediate threat. *Convolvulus arvensis* and *Aegilops cylindrica* threaten at least one occurrence of *O. harringtonii*, and the former is listed among the top ten noxious weeds in Colorado (Colorado's Noxious Weed Management Program undated). Other invasive species recorded at one or more occurrences include *Descurainia* spp., prickly Russian thistle (*Salsola tragus*), and *Bromus tectorum*. An unidentified *Lepidium* species was also been reported at one occurrence (Occurrence 10, **Table 1**; Colorado Natural Heritage Program 2002). If the *Lepidium* species refers to *L. latifolium*, it is a particular cause for concern because this is a tall, aggressive, perennial species of noxious weed that has a widely spreading root system. Unfortunately, the herbicides used to control dicot species of weeds are also likely to be detrimental to *O. harringtonii*.

Oenothera harringtonii relies on insect pollinators and is therefore vulnerable to declines in its pollinator populations. Pesticide use, habitat alteration and fragmentation, and the introduction of non-native plants and animals all contribute to reducing pollinator population size as well as causing the extirpation or extinction of pollinator species (Bond 1995). Pesticides that are considered safe for humans but specifically target Lepidopteran pests such as hornworms might be a particular problem where the urban community is growing. *Bacillus thuringiensis* (Bt) is often perceived as a benign pesticide safe for home use (Cranshaw 1998). However, since its targets are often members of the Lepidoptera, its increased use may be cause for particular concern. Hornworms, the larval stage of *Hyles lineata* and other hawkmoths, are particularly susceptible to Bt (Cranshaw 1998). Although it may be argued that plant species dependent upon specific pollinator species may be the most vulnerable, and that the relative variety of pollinator species for *O. harringtonii* confers some buffer to pollinator loss, other factors may be just as important. For example, the small, relatively few numbers of flowers per *O. harringtonii* occurrence site suggest that they may not be very competitive when attracting pollinators from a shrinking pool of insect vectors. In addition, Bond (1995) makes the argument that when the diversity of threats is sufficiently high, whole assemblages of mutualists may be eliminated and that no mutualistic relationship is completely guaranteed.

At the present time there is only one documented occurrence of *Oenothera harringtonii* on National Forest System land within Region 2 (Occurrence 16,

Table 1). There is insufficient information to evaluate all of the specific threats to this population, but it is known to be within a grazing allotment and likely part of the occurrence is in a right-of-way. Seed production is likely to be particularly negatively affected if livestock use the plants during its reproductive period and consume the flowers or seeds. *Oenothera* species are often palatable to livestock. For example, *O. organensis* is grazed by livestock disproportionately to its abundance in southern New Mexico (author's observation at times during 1991 to 1996). Highway maintenance activities may impact part of the population. The population on National Forest System land is also likely be vulnerable to the encroachment of invasive weeds. Herbicides, particularly those that target dicots, are likely to kill *O. harringtonii*. Mowing before germination and after seed set may be a viable option in controlling invasive weeds within its habitat. Cultivation (tilling) is not a good alternative until the consequences of such high-intensity disturbance are better understood.

Natural catastrophes and environmental stochasticity appear to represent less imminent threats, given the habitat requirements and geographic location of *Oenothera harringtonii*. It is unclear how global climate change may affect this species. In the last one hundred years, the average temperature in Fort Collins, Colorado has increased 4.1 °F, and precipitation has decreased by up to 20 percent in central parts of the state. Based on projections made by the Intergovernmental Panel on Climate Change and results from the United Kingdom Hadley Centre's climate model (HadCM2), by 2100 temperatures in Colorado could increase by 3 to 4 °F in spring and fall, with a range of 1 to 8 °F, and 5 to 6 °F in summer and winter with a range of 2 to 12 °F (U.S. Environmental Protection Agency 1997). These changes may not have a profound effect on *O. harringtonii* because it is apparently adapted to xeric conditions. It is also likely able to tolerate the potentially wide year-to-year variation in growing conditions since it produces high numbers of seeds that are believed to be long-lived in the seed bank. Substantial seed longevity is inferred from its growing in areas that have experienced recent disturbance. Observations made at Fort Carson suggest that drought may be more detrimental than would be expected considering its naturally xeric habitat. Plants have not been observed at known occurrence sites since 2001, which was prior to a significant drought that was believed largely responsible for the loss (Rifici personal communication 2003). Subsequent observations of these sites will be valuable in providing more information on the population dynamics of this species.

No molecular analyses have been made on the genetic structure of *Oenothera harringtonii*. Individuals exhibit quite a large degree of morphological heterogeneity within the same population (Goeken 1968) although this may not necessarily reflect genetic heterogeneity. The extent of genetic variation in *O. harringtonii* is difficult to predict. Another self-incompatible, narrow endemic, perennial *Oenothera* species, *O. organensis*, is allozymically depauperate (Levin et al. 1979). Fifteen loci were examined, but only one was polymorphic and that was only found to have two alleles. On the other hand, *O. argillicola*, which is a short-lived perennial endemic to Appalachia and also grows in barren shale habitats, exhibits a moderate degree of genetic variation (Kruckenberg and Rabinowitz 1985).

Similarly, few comments can be made on the influence of demographic stochasticity on individual populations, principally because there is no information on the survival probability of individuals at any given life-stage or age (see Demography section). Holsinger and Gottlieb (1991) suggest that demographic factors may be more significant than genetic factors for a rare species whose distribution and abundance has not been altered. However, the extent to which the abundance and range of *Oenothera harringtonii* has been altered by the considerable development is not documented, and any loss in genetic diversity within the species is unknown. There is some evidence that *O. harringtonii* shares some of the characteristics of *O. avita* ssp. *eurekaensis*, which was studied in detail by Pavlik and Barbour (1988; see Demography section). They concluded that factors threatening the populations were extrinsic rather than genetic.

The loss of genetic integrity by hybridization does not appear to be a significant threat. Although controlled hybridization experiments between *Oenothera harringtonii* and other members of the *O. caespitosa* complex have easily produced hybrids, little or no evidence exists that significant hybridization naturally occurs (see Reproductive biology and autecology section; Goeken 1968, Stockhouse 1973, Wagner et al. 1985). Typically, *O. harringtonii* is isolated from related species by virtue of its habitat. It shares the same habitat with *O. caespitosa* ssp. *macroglottis* in only one part of its range. In this case, a form of mechanical isolation is likely to exist that prevents effective pollen transfer (Grant 1981). Differences in the structural characteristics of the flowers apparently attract a different suite of arthropod pollinators (see

Reproductive biology and autecology section and Community ecology section).

In summary, extrinsic factors such as urbanization, mining, recreation, weed competition, and livestock grazing are likely the primary range-wide threats to *Oenothera harringtonii*, but their impacts need to be better defined. The threats and malentities identified for this report appear to be very interrelated, and a clear envirogram was difficult to construct (**Figure 7**). Habitat loss is the most significant concern, but it has a variety of causes. Disturbance that results in habitat loss and that contributes to excessive soil erosion (such as that imposed by urban development and mining activities) is clearly deleterious. Activity from other agents of frequent disturbance such as vehicle traffic and livestock grazing also contribute to the spread of invasive non-native plant species (weeds), which also appears to be a substantial threat. Weeds are direct competitors for resources such as water, nutrients, and light; also many weed species secrete allelopathic chemicals into the soil, which may contribute to habitat loss (Sheley and Petroff 1999). Herbicides are generally applied to control the spread of weeds, but many of these are deleterious to *Oenothera* species. In addition, although pesticides primarily contribute to pollinator decline, herbicides can also have a detrimental effect on some arthropods. The extent and duration of the malentities are also important factors and need further study.

Conservation Status of the Species in Region 2

The cumulative impact of disturbance, land conversion, and land management practices on the abundance and distribution of *Oenothera harringtonii* cannot be accurately estimated because of inadequate historical records. Only one occurrence has been documented on National Forest System lands within Region 2, namely that on the Comanche National Grassland (Occurrence 16, **Table 1**). This occurrence was found in 1995, and although the area has been searched occasionally since that time, *O. harringtonii* plants have not been observed again (Olson personal communication 2004). Another occurrence (Occurrence 17, **Table 1**) has been reported to be relatively near the boundary of the Comanche National Grassland but not within it.

Management of the Species in Region 2

Implications and potential conservation elements

Management plans have not specifically addressed this species. *Oenothera harringtonii* is exposed to livestock grazing pressures and occasional prescribed burns at the known occurrence site on the Comanche National Grassland (Olson personal communication 2004). The consequences of any aspect of these activities on the *O. harringtonii* population have not been documented. Livestock grazing, especially during flowering and fruiting, may limit the number of seeds *O. harringtonii* can produce. Livestock also contribute to the spread of non-native invasive plant species (see Threats section). Considering the areas in which it grows, the seeds appear to germinate in response to some types of disturbance. However, the problem is that there is little information on which to base predictions as to its response to specific disturbance types or levels. For example, the soil disturbance generated by transient livestock grazing is generally far less than that around a salt lick. In this case, the type of livestock use has to be evaluated, not just livestock use *per se*. *Oenothera harringtonii* may well be excluded from the community if disturbance is too frequent or too much (see Demography section). One consideration in predicting the potential effect of fire on *O. harringtonii* is that the species is adapted to barren shale and gravelly areas that are historically unlikely to have experienced much litter accumulation. Therefore, unlike typical grassland species, its habitat likely experienced only infrequent, cool-temperature burns.

Habitat invasion by non-native plant species likely contributes to loss of habitat. *Oenothera harringtonii* is likely to be uncompetitive and may be directly out-competed by non-native plant species. Two classes of weeds pose a threat at current occurrences (**Table 3**). Those defined as noxious weeds, such as *Convolvulus arvensis* and *Aegilops cylindrical*, and those non-native species used for agriculture and restoration that have escaped, such as *Melilotis* spp. and *Kochia scoparia*. No weeds have been reported in occurrences on National Forest System land, but the dynamic nature of weed infestations makes it necessary to be vigilant. Weed control methods pose their own problems. Herbicides,

particularly those that target dicots, are also likely to kill *Oenothera* species. Mechanical methods to control or eliminate weeds can be considered, and mowing after flowering and capsule maturation may be a viable option. However, cultivation (tilling) that has been used in the past to re-vegetate National Forest System land is not a good alternative until the consequences of such disturbance are better understood. If cultivation is attempted, then saving some seeds/capsules for a reseeding effort may be considered.

Successful *Oenothera harringtonii* reproduction may be vulnerable to a decline in hawkmoth and bee pollinators. The use of pesticides on agricultural land and in the rapidly expanding urban areas can impact local pollinator populations on nearby land that is not directly exposed to pesticides.

When considering which populations to protect, it is important to remember that species often exhibit genetic differences between populations. Even though *Oenothera harringtonii* is cross-pollinated, its relatively few and isolated populations suggest that there is the potential for local ecotypes to have adapted to narrow edaphic conditions. Small populations may be genetically depauperate as a result of changes in gene frequencies due to inbreeding, or founder effects (Menges 1991), but the value of small populations should not be belittled. For example, alleles that were absent in larger populations were only found in a small population of *Astragalus osterhoutii* (Karron et al. 1988). Therefore, in order to conserve genetic variability, in the absence of genetic (DNA) data, it is likely most important to conserve as many populations as possible in as large a geographic area as possible and that a larger population is not automatically better. Maintaining abundant and healthy pollinators is vitally important to population sustainability because it is an obligate cross-pollinator and seed production appears a critical step in its life cycle (see Reproductive biology and autecology section and Community ecology section).

Tools and practices

Documented inventory and monitoring activities are needed to clarify the status and vulnerability of *Oenothera harringtonii*. Most of the occurrence information is derived from herbarium specimens or relatively casual observations by botanists and does not provide quantitative information on the abundance or spatial extent of the populations. In addition, there is little information on population structure, persistence of either individuals or populations, or information on its reproductive biology.

Species inventory

Inventory activities are important for this species. It is unlikely that it would be mistaken for other species of *Oenothera* although it is in sympatry with ssp. *macroglottis* in Fremont County. It also grows in the same general region, although not in the same habitat, as the widespread white-flowered species, *O. coronopifolia* and *O. albicaulis*. The current field survey forms for endangered, threatened, or sensitive plant species used by the Colorado Natural Heritage Program (CNHP undated) request the collection of data that is appropriate for inventory purposes. The number of individuals, the area they occupy, and the apparent potential habitat are important data for occurrence comparison. The easiest way to describe populations over a large area may be to count patches, making note of their extent, and to estimate or count the numbers of individuals within patches. Collecting information on flowering plants versus rosettes is also valuable in assessing the vigor and likely sustainability of a population. Recording observations on habitat will provide valuable information.

Habitat inventory

There is an inadequate understanding of all the features that comprise “potential” habitat to be able to make a rigorous inventory of areas that will actually be colonized. At the current time, potential habitat is best defined as habitat that, from casual observation, appears suitable for the species, but which is not occupied by it. The available information on habitat supplied with descriptions of occurrences is generally insufficient to make accurate analyses of the habitat that is currently available for colonization. The available habitat descriptions suggest that, within the restrictions of geology and the eco-climate zones in which it exists, this species grows in a variety of low-competition habitats. There are no studies that relate the abundance or vigor of populations to habitat conditions, which is an important consideration when making a habitat inventory for a species.

Population monitoring

No monitoring or demographic studies have been reported. Lesica (1987) has discussed a technique for monitoring non-rhizomatous, perennial plant species using permanent belt transects. Permanent transects may be the most accurate way to study long-term trends. Elzinga et al. (1998) and Goldsmith (1991) have discussed using a rectangular quadrant frame along transect lines to effectively monitor the

“clumped-gradient nature” of populations that would apply to some *Oenothera harringtonii* populations. It is important to monitor the areas between sub-populations, along a road right-of-way for instance, as the population dynamics are not known and shifts in stands within a population need to be identified. A series of colonizations and localized extirpations would be expected for a relatively short-lived plant species.

Information on size, or size class, of the plants in addition to estimated age needs to be included in the monitoring design (Gross 1981). For example, the term “rosette” is far more descriptive than the term “young.” If all individuals are annual, the size and flowering status is important because some individuals may never flower and contribute to long-term survival of the species. Habitat conditions, such as soils, slope, aspect, elements of disturbance, available moisture and associated vegetation, need to be noted as part of the monitoring scheme.

The use of photopoints and photoplots is recommended. Photographic documentation is very useful in visualizing vegetation changes over time and is increasingly used in monitoring plans. Photopoints are collections of photographs of the same field of view that have been retaken from the same position over some given time period. Photoplots are usually relatively close-up photographs showing a birds-eye view of the monitoring plot. In both cases, a rebar or some other permanent marker need to be placed to mark the location where the photographer stands, and compass directions and field-of-view details must be recorded to make sure the photograph can be accurately retaken. Even though digital copies are convenient and easy to store, for example on CDs, many museums and researchers suggest storing additional slides or even hardcopies as in 50 years time the technology to read media such as memory sticks and CDs may no longer be available.

Habitat monitoring

The lack of information on habitat requirements makes it premature to consider that habitat monitoring in the absence of plants can effectively occur. Habitat monitoring in the presence of plant occurrences needs to be associated with population monitoring protocols. Descriptions of habitat always need to be recorded during population monitoring activities in order to link environmental conditions with abundance over the long term. Conditions several years prior to the onset of a decrease or increase in population size may be more important than conditions existing during the year the

change is observed. Current land use designation and evidence of land use activities, for example hiking, biking, or livestock grazing, are important to include with the monitoring data.

Population or habitat management approaches

There have been no systematic monitoring programs for this species and no documented attempts of active management. Beneficial management practices that have been generally implemented within national forests and in some state parks include restricting recreational vehicle traffic and routing hikers to designated trails. Monitoring the populations in these protected areas would be a necessary step in determining the benefits of protection measures.

Information Needs

Oenothera harringtonii is a rare species that appears to be limited to specific soil types in a relatively small geographic area in south-central Colorado. Inventory and monitoring of existing sites appear to be the most important needs. Monitoring pre-existing sites is essential in order to understand the implications of existing and new management practices. Where management practices are likely to change, inventory needs to be taken to collect baseline data and periodic monitoring needs to be conducted after the new policy is initiated. In addition, the life cycle characteristics of this species need to be confirmed, preferably through published studies. This is a very important piece of biological information and could be obtained as part of the monitoring activities. Creating a comprehensive inventory of this species will aid in evaluating the vulnerability of the species to local extirpations and eventual extinction. A study on the genetic structure of populations at the geographic limits of its range would determine how homogenous the species is and provide information on its genetic vulnerability. Specific information on the pollinator species and their behavior would assist in assessing the vulnerability of the species to pollinator reduction.

Habitat requirements need to be more rigorously defined. It is unclear as to what constitutes potential habitat. The shale soils it prefers support early successional communities with low vegetation cover and are naturally susceptible to erosion and sheet flooding. The importance of disturbance due to these typical environmental processes and to wildlife that generate localized soil disturbance (i.e., gophers and prairie dogs) is not known. The impacts of disturbance by large ungulates and anthropogenic activities are also

not known. *Oenothera harringtonii*'s ability to tolerate competition is speculated as being very low because it grows in areas with low vegetative cover. It is also thought to tolerate anthropogenic disturbance because it has been found on highway rights-of-way and road cuts. Both of these hypotheses need to be confirmed. Studies are also needed to understand the influence of the intensity and timing of the different types of disturbance on population establishment and longevity.

It is unknown whether *Oenothera harringtonii* colonizes disturbed habitats from seed dispersed from populations away from the site of disturbance, or whether seedlings are derived from the existing seed bank. If colonization is from seed rain, the absence of competitive plant species may be a significant factor in the colonization process. Alternatively, if the seed is from that in the seed bank, this suggests that seed may be prompted to germinate by soil disturbance. Answers to these questions will contribute to gaining a better understanding of the population dynamics of this taxon. The rate of colonization and the availability of preferred habitat influence how populations recover after significant disturbance.

There have been no documented attempts at artificially establishing new populations or of including this species in vegetation restoration efforts. Available information suggests that seeding an area may meet with success, but transplanting the species may not be viable. Although some information on cultivating this species is available, it may not be completely transferable to restoring or creating wild populations. Therefore, some research would need to be carried out before such a project could be undertaken.

The current understanding of the reproductive biology of *Oenothera harringtonii* is primarily based upon comparisons with other members of the *O. caespitosa* complex. Management practices may need to be modified if limited or specialized pollinator species are found to be essential for cross-pollination. The factors that limit population size and abundance and that contribute to the variable occurrence sizes are not known and need to be determined.

In summary, the information needs for *Oenothera harringtonii* are:

- ❖ Inventory occurrences, especially within Region 2;
- ❖ Monitor occurrences on a yearly basis to determine long-term population trends;
- ❖ Clarify life cycle characteristics;
- ❖ Determine characteristics of and map potential habitat;
- ❖ Define the significance of disturbance in the species' life history;
- ❖ Investigate interactions between invasive non-native plant species and *Oenothera harringtonii*;
- ❖ Investigate pollination biology characteristics;
- ❖ Clarify the factors that limit the population size and abundance of the species.

DEFINITIONS

Adaxial — The side nearest to or facing toward the axis of an organ or organism; “the upper side of a leaf is known as the adaxial surface” (Allaby 1992).

Annual — A plant that completes its entire life cycle within the space of a year.

Biennial — A plant having a life cycle that normally takes two seasons from germination to death to complete; flowering biennials usually bloom and fruit in the second season.

Bivalents — Applied to two homologous chromosomes when they are paired during a specific phase (the prophase) of the first meiotic division.

Dicot — A flowering plant with two cotyledons, as opposed to only one cotyledon such as a grass. A dicot is also called a “forb.”

Edaphic — Relating to soil, especially as it affects living organisms.

Herkogamy — Spatial separation of male and female reproductive elements by a hermaphroditic organism in order to ensure cross pollination.

Homologous — In the context of this assessment: homologous chromosomes are those that contain identical linear sequences of genes and pair during meiosis (Allaby 1992).

Hydrochasy — Opening induced by wet conditions.

Hydrochory — Seed dispersal by flowing water.

Oligolectic — Bee species in which females restrict pollen collecting to one or a few related plant species are called oligolectic species (Eickwort and Ginsberg 1980).

Ombrohydrochory — Seed dispersal by rain.

Outcrossing — Cross pollination (controlled or natural) among unrelated individuals.

Malentity — A malentity, when in contact with the subject organism, is capable of having an adverse affect on that organism with no adverse consequence to itself. A malentity can adversely influence the subject organism accidentally (e.g., rain causing a flash flood) or intentionally (e.g., a herbicide).

Monocarpic — Plants that flower and produce fruit only once during their life cycle, after which they die. Most annual plants and biennial plants are monocarpic, but there are also a small number of monocarpic perennial plants that flower just once, sometimes after decades, and die soon afterwards,

Myrmecchory — Seed dispersal by ants.

Perennial — A plant that lives for more than two seasons and after some initial period produces flowers annually (Allaby 1992).

Pollinators:

Hawkmoth:	<i>Hyles lineata</i> Fabricius synonym: <i>Celerio lineata</i> Fabricius <i>Manduca quinquemaculata</i> Haworth
Oligolectic bee:	<i>Adrena anograe knowltoni</i> Linsley and Swain <i>Lasioglossum (Sphecodagastra) texanum</i> Cresson
Polylectic bee:	<i>Lasioglossum sisymbrii</i> Cockerell <i>Lasioglossum trizonatum</i> Cresson

Polylectic — A bee which visits many different plants for pollen (and nectar). Compare “oligolectic.”

Ranks — NatureServe and the Heritage Programs Ranking system. Internet site: <http://www.natureserve.org/explorer/granks.htm>

G2 — Imperiled globally because of rarity or because of some factor(s) making it very vulnerable to extinction or elimination. Typically 6 to 20 occurrences or few remaining individuals (1,000 to 3,000) or acres (2,000 to 10,000) or linear miles (10 to 50).

S2 — Imperiled in the nation or subnation because of rarity or because of some factor(s) making it very vulnerable to extirpation from the nation or subnation. Typically 6 to 20 occurrences or few remaining individuals (1,000 to 3,000).

Self-incompatible — Incapable of self-fertilization.

Semelparous — Reproducing once and then dying.

Tachyspory — The seeds are set free immediately after maturation.

Xerochasy — Opening induced by dry conditions.

COMMONLY USED SYNONYMS OF PLANT SPECIES

Commonly used synonyms of plant species mentioned in this report (Kartesz 1994). The reference in parenthesis refers to a flora in Region 2 in which the synonym is used:

<i>Chaetopappa ericoides</i>	<i>Leucelene ericoides</i> (Weber and Wittmann 2001)
<i>Euphorbia lata</i>	<i>Chamaesyce lata</i> (Weber and Wittmann 2001)
<i>Eurotia lanata</i>	<i>Krascheninnikovia lanata</i> (Weber and Wittmann 2001)
<i>Haplopappus fremontii</i>	<i>Oönothis foliosa</i> (Weber and Wittmann 2001)
<i>Hymenoxys acaulis</i>	<i>Tetrandeum acaulis</i> (Weber and Wittmann 2001)
<i>Oenothera caespitosa</i> ssp. <i>macroglottis</i>	<i>Oenothera caespitosa</i> ssp. <i>montana</i>
<i>Oenothera caespitosa</i> ssp. <i>macroglottis</i>	<i>Pachylophus caulescens</i>
<i>Oenothera caespitosa</i> ssp. <i>marginata</i>	<i>Oenothera eximia</i>
<i>Oenothera caespitosa</i> ssp. <i>marginata</i>	<i>Oenothera caespitosa</i> ssp. <i>montana</i> pro parte
<i>Oryzopsis hymenoides</i>	<i>Achnatherum hymenoides</i> (Weber and Wittmann 2001)
<i>Psoralea tenuiflora</i>	<i>Psoralidium tenuiflorum</i> (Weber and Wittmann 2001)
<i>Sophora nuttalliana</i>	<i>Vixibia nuttalliana</i> (Weber and Wittmann 2001)

REFERENCES

- Allaby, M. 1992. The concise Oxford dictionary of botany. Oxford University Press, New York, NY.
- Andrewartha, H.G. and L.C. Birch. 1984. The ecological web: more on the distribution and abundance of animals. University of Chicago Press, Chicago, IL.
- Belew, G. 2003. Natural and Cultural Resources Division, Fort Carson's Environmental Management Program, Department of Defense. Personal communication.
- Bond, W.J. 1995. Assessing the risk of plant extinction due to pollinator and disperser failure. *In*: J.H. Lawton and R.M. May, editors. Extinction rates. Oxford University Press, New York, NY.
- Brekke, Erik. 2003. Bureau of Land Management - Royal Gorge Field Office, Cañon City, Colorado. Personal communication.
- Bureau of Land Management. 2000. BLM Colorado State Office Director's Sensitive Species List (Animals and Plants) June, 2000 & Plants in Colorado Federally listed as Threatened or Endangered and Candidates for Listing. Internet sites: http://www.co.blm.gov/botany/sens_species.htm; <http://www.co.blm.gov/botany/listedtb.htm> [Accessed December 2004].
- Callaway, R.M. and E.T. Ascheloug. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290:521–523.
- Carsey, K. 1996. Middle Arkansas Valley – Pueblo and Fremont Counties. Unpublished Site Evaluation Form – Colorado Natural Areas Program, Denver, CO.
- Cleland, R.E. 1957. Chromosome structure in *Oenothera* and its effect on the evolution of the genus. *Proceedings of the International Genetics Symposium (Supplement to Cytology)*. 1956:5-19.
- Cleland, R.E. 1972. *Oenothera* - Cytogenetics and evolution. Academic Press, New York, NY.
- Colorado Division of Mining and Geology 2003. 4/1/2003 Agenda Reports. For example, 4/1/2003 Agenda Report For the period 3/1/2003 thru 3/31/2003. Internet site: <http://mining.state.co.us> [Accessed December 2004].
- Colorado Natural Areas Program. 1989. Preserve design for Portland, Fremont County, Colorado. Date of site design. January 10, 1989. Unpublished document Colorado Natural Areas Program, Denver, CO.
- Colorado Natural Heritage Program. 2002. Data compilation for *JnJ Associates* LLC, completed September 2002. Unpublished report. Colorado Natural Heritage Program, Colorado State University, Fort Collins, CO.
- Colorado Natural Heritage Program On-line Rare Plant Guide, Fort Collins, Colorado. Internet site: <http://ndis.nrel.colostate.edu/ndis/rareplants> [Accessed January, 2003].
- Colorado Natural Heritage Program. Data Requests and Environmental Review section, Colorado Natural Heritage Program Biological and Conservation Data system, Fort Collins, Colorado. Internet site: <http://www.cnhp.colostate.edu/er.html#data>.
- Colorado's Noxious Weed Management Program. Undated. Colorado Department of Agriculture, Lakewood, Colorado. Internet site: http://www.colostate.edu/Depts/SoilCrop/extension/CEPEP/noxious_weeds.htm [Accessed May 2003].
- Cranshaw, W. 1998. Pests of the West. Fulcrum Publishing, Golden, CO.
- Denver & Rio Grande Western Railroad. 1936. Rio Grande Guide to Romantic Rocky Mountain Wonderlands. Summarized Reproduction © 2000 Sandia Software All Rights Reserved. Internet site: <http://ghostdepot.com/rg/guide%20book/guidebook.htm> [Accessed October 2004].
- Eickwort, G.C. and H.S. Ginsberg 1980. Foraging and Mating Behavior in Apoidea. *Annual Review of Entomology* 25:421-446.
- Elzinga, C.L., D.W. Salzer and J.W. Willoughby. 1998. Measuring and monitoring plant populations. Bureau of Land Management Technical Reference 1730-1. U.S. Department of Interior, Bureau of Land Management, Denver, CO.

- Federal Highways Administration, U.S. Fish and Wildlife Service, Colorado Department of Natural Resources (DNR), Colorado DNR Division of Wildlife, Colorado Department of Transportation, and The Nature Conservancy. 2002, updated 2004. Memorandum of Agreement among the Colorado Department of Transportation, Federal Highway Administration, the U.S. Fish and Wildlife Service, Colorado Department of Natural Resources (DNR), Colorado DNR Division of Wildlife and The Nature Conservancy. Published on the Internet site: <http://www.fhwa.dot.gov/environment/strmlng/comoa.htm> [Accessed February 2003, November 2004].
- Fenner, M. 1992. Seeds. The ecology of regeneration in plant communities. CAB International, Wallingford, Oxford, England.
- Goeken, R. 1968. Biosystematics of *Oenothera caespitosa* subspecies *crinita*, *eximia*, *marginata*, and *montana*. Unpublished MS Thesis, Colorado State University, Fort Collins, CO.
- Goldsmith, F.B. 1991. Monitoring for conservation and ecology. Chapman and Hall, New York, NY.
- Grant, V. 1981. Plant speciation. Second Edition. Columbia University Press, New York, NY.
- Gray, A. 1849. *Pachylophus eximia*. Plantae Fendlerianae Novi-Mexicanae. Memoirs of the American Academy of Arts and Sciences Series 2, 1(art.1): p 45.
- Green, T.W. and I.G. Palmblad. 1975. Effects of insect seed predators on *Astragalus cibarius* and *Astragalus utahensis* (Leguminosae). Ecology 56:1435-1440.
- Gregory, D.P. 1964a. Hawkmoth pollination in the genus *Oenothera*. Aliso. 5(6):357-384.
- Gregory, D.P. 1964b. Hawkmoth pollination in the genus *Oenothera*. Aliso. 5(6):385-419.
- Grime, J.P., J.G. Hodgson, and R. Hunt. 1988. Comparative plant ecology – a functional approach to common British species. Allen and Unwin, Inc., Winchester, MA.
- Gross, K.L. 1981. Predictions of fate from rosette size in four “biennial” plant species: *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota*, and *Tragopogon dubius*. Oecologia 48:209-213.
- Guralnik, D. 1982. Webster’s New World Dictionary. Simon and Schuster, New York, NY.
- Harper, J.L. 1977. Population biology of plants. Academic Press, New York, NY.
- Harper, J.L. and J. White. 1974. The demography of plants. Annual Reviews Ecology and Systematics 5:419-463.
- Hazlett, D.L. 1997. The Comanche National Grassland: A preliminary survey for threatened and endangered plant species. Unpublished document. USDA Forest Service Comanche National Grassland, La Junta, CO.
- Hazlett, D.L. 2000. Plant species of the Comanche National Grasslands: A working checklist. Unpublished document. USDA Forest Service Comanche National Grassland, Springfield, CO.
- Hazlett, Donald L. 2004. Vascular plant species of the Comanche National Grassland in southeastern Colorado. General Technical Report RMRS-GTR-130. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Fort Collins, CO.
- Hirose T. and N. Kachi. 1982. Critical plant size for flowering in biennials with special reference to their distribution in a sand dune system. Oecologia 55:281-284.
- Holsinger, K.E. and L.D. Gottlieb. 1991. Conservation of rare and endangered plants: principles and prospects. Pages 195-208 in D.A. Falk and K.E. Holsinger, editors. Genetics and conservation of rare plants. Oxford University Press, New York, NY.
- Joern, A. and K.H. Keeler. 1995. The changing prairie – North American Grasslands. Oxford University Press, New York, NY.
- Karron J.D. 1991. Patterns of genetic variation and breeding systems in rare plant species. Pages 87-98 in D.A. Falk and K.E. Holsinger, editors. Genetics and conservation of rare plants. Oxford University Press, New York, NY.

- Karron, J.D., Y.B. Linhart, C.A. Chaulk, and C.A. Robertson. 1988. Genetic structure of geographically restricted and wide-spread species of *Astragalus* (Fabaceae). *American Journal of Botany* 75:1114-1119.
- Kartesz, J. 1994. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland. Volume 1 - Checklist. Second Edition. Timber Press, Portland, OR.
- Kelso, Sylvia (Tass). 2003. Associate Professor, Colorado College, Colorado Springs, CO. Personal communication.
- Klironomos, J.N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417:67-70.
- Klironomos, J.N. 2003. Variation in response to native and exotic arbuscular mycorrhizal fungi. *Ecology* 84(9): 2292-2301.
- Kruckenbergh, A.R. and D. Rabinowitz. 1985. Biological aspects of endemism in higher plants. *Annual reviews of Ecology and Systematics* 16:447-479.
- Ladyman, J.A.R. 2000. Progress Report - Development of management strategies for protected plant species in highway right-of-ways. Unpublished report. Prepared for and submitted to the New Mexico State Highway and Transportation Dept., Santa Fe, NM.
- Lammon, John. 2003. USDA Forest Service, La Junta, CO. Personal communication.
- Laurenroth, W.K. and D.G. Milchunas. 1992. Short-grass steppe. Pages 183-362 in R.T. Coupland, editor. *Ecosystems of the world Vol. 8A: Natural grasslands, Introduction and western hemisphere*. Elsevier, New York, NY.
- Levin, D.A., K. Ritter, and N.C. Ellstrand. 1979. Protein polymorphism in the narrow endemic *Oenothera organensis*. *Evolution* 33(2):534-542.
- Lesica, P. 1987. A technique for monitoring non-rhizomatous, perennial plant species in permanent belt transects. *Natural Areas Journal* 7(2):65-68.
- Levin, R.A., W.L. Wagner, P.C. Hoch, W.J. Hahn, A. Rodriguez, D.A. Baum, L. Katinas, E.A. Zimmer, and K.J. Sytsma. 2004. Paraphyly in Tribe Onagreae: Insights into phylogenetic relationships of Onagraceae based on nuclear and chloroplast sequence data. *Systematic Botany* 29:147-164.
- Linsley, E.G., J.W. MacSwain, and P.H. Raven. 1963. Comparative behavior of bees and Onagraceae. II. University of California publications in entomology 33:25-58.
- MacArthur, R.H. and E.D. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.
- Mancuso, M. and R.K. Moseley. 1993. Report on the conservation status of *Astragalus yoder-williamsii* in Idaho. The Idaho Conservation Data Center, Nongame and Endangered Wildlife Program, Idaho Department of Fish and Game, Boise, ID.
- McGregor, R.L. and members of the Great Plains Flora Association, editors. 1986. *Flora of the Great Plains*. University of Kansas Press, Lawrence, KS.
- Menges, E.S. 1991. The application of minimum viable population theory to plants. Pages 45-61 in D.A. Falk and K.E. Holsinger, editors. *Genetics and conservation of rare plants*. Oxford University Press, New York, NY.
- Mullis, Monique. 2003. Lake Pueblo State Park, Pueblo, CO. Personal communication.
- Munz, P.A. 1931. Studies in Onagraceae VII. The subgenus *Pachylophus* of the genus *Oenothera*. *American Journal of Botany* 18:728-738.
- NatureServe Web site. Version 1.6 (03 December 2001). Data last updated November 2001. Global Heritage Status Rank assigned 05 January 1998 with Global Ranking Factors Edition Date: 17 May 1996. National Heritage Status Rank assigned 22 Dec 1997. Internet site: http://www.natureserve.org/explorer/servlet/NatureServe?loadTemplate=tabular_report.wmt&paging=home&save=all&sourceTemplate=reviewMiddle.wmt [Accessed June 12, 2003].
- New York Botanical Garden. Herbarium records. Internet site: <http://scisun.nybg.org:8890/> [Accessed May 2003].

- National Oceanic and Atmospheric Administration. 2004. CoRIS - NOAA's Coral Reef Information System (<http://coris.noaa.gov/welcome.html>). Glossary section. Internet site: <http://www6.nos.noaa.gov/coris/glossary.lasso?letter=p> [Accessed July2004].
- Olf, H., B. Hoorens, R.G.M. de Goede, W.H. van der Putten, and J.M. Gleichman. 2000. Small-scale shifting mosaics of two dominant grassland species: the possible role of soil-borne pathogens. *Oecologia* 125:45–54.
- Olson, Steven. 2004. USDA Forest Service Pike-San Isabel National Forests and Cimarron-Comanche National Grasslands. Personal communication.
- Osborne, J.L., S.J. Clark, R. Morris, I. Williams, R. Riley, A. Smith, D. Reynolds, and A. Edwards. 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology*. 36:519-533.
- Pake, C.E. and D.L. Venable. 1996. Seed banks in desert annuals: Implications for persistence and coexistence in a variable environment. *Ecology* 77:1427-1435.
- Pavlik, B.M. and M.G. Barbour. 1988. Demographic monitoring of endemic sand dune plants, Eureka Valley, California. *Biological Conservation* 46:217-242.
- Poppendieck, H.H.1995. Hygrochastic capsules in *Oenothera* (Onagraceae). *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* 25:99-115.
- Powell, Jerry. 2003. Colorado Department of Transportation, Denver, CO. Personal communication.
- Raguso, R.A. 2003. Assistant Professor, Department of Biology, University of South Carolina Personal communication.
- Raven, P.H. 1962. The systematics of *Oenothera* subgenus *Chylisma*. *University of California Publications in Botany* 34:1-122.
- Raven, P.H. 1979. A survey of reproductive biology in Onagraceae. *New Zealand Journal of Botany* 17:575-793.
- Rifici, Karen. 2003. Natural and Cultural Resources Division, Fort Carson's Environmental Management Program, Department of Defense. Personal communication.
- Russell, J. and D.A. Levin. 1988. Competitive relationships of *Oenothera* species with different recombination systems. *American Journal of Botany* 75:1175-1180.
- Rydberg, P.A. 1903. *Pachylophus exiguus* in Rocky Mountain Flora. *Torrey Botanical Club* 30:260.
- Shaw, R.B., S.L. Anderson, K.A. Schultz, and V.E. Diersing. 1989. Floral inventory for the U.S. Army Pinon Canyon Maneuver Site, Colorado. *Phytologia* 67(1):1-42.
- Sheley, R.L. and J.K. Petroff.1999. Biology and management of noxious rangeland weeds. Oregon State University Press, Corvallis, OR.
- Silvertown, J., M. Franco, I. Piasanty, and A. Mendoza. 1993. Comparative plant demography – relative importance of life cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* 81:465-476.
- Spackman Panjabi, S.C. 2004. Visiting insect diversity and visitation rates for seven globally-imperiled plant species in Colorado's middle Arkansas Valley. Unpublished document. Colorado Natural Heritage Program, Colorado State University Ft. Collins, Colorado, prepared for Native Plant Conservation Alliance National Fish and Wildlife Foundation May 2004. Accessible at Internet site: <http://www.cnhp.colostate.edu/reports.html>.
- Spackman, S., B. Jennings, J. Coles, C. Dawson, M. Minton, A. Kratz, and C. Spurrier. 1997. Colorado Rare Plant Field Guide. Prepared for the Bureau of Land Management, The USDA Forest Service, and the U.S. Fish and Wildlife Service by the Colorado Natural Heritage Program, Fort Collins, CO.
- Stanley, R.G. and H.F. Linskens. 1974. Pollen, biology, biochemistry, management. Springer-Verlag, New York, NY.
- Stockhouse, R.E. 1973. Biosystematic studies of *Oenothera* L. subgenus *Pachylophus*. Unpublished Ph.D. Dissertation, Colorado State University, Fort Collins, CO.

- Stockhouse, R. 2003. Pacific University, Forest Grove, OR. Personal communication.
- Tiemann, Jeff. 2003. Colorado State Parks, Denver, CO. Personal communication.
- Trevis, L. 1958. Interrelations between the harvester ant *Vermessor pergandei* (Mayr) and some desert ephemerals. *Ecology* 39:695-704.
- Tweto, O. 1979. Geologic map of Colorado. U.S. Geological Survey, Denver, CO.
- USDA Forest Service. 1995. Forest Service Manual, Title 2600-Wildlife, Fish and Sensitive Plant Habitat Management. USDA Forest Service, Washington, D.C.
- USDA Forest Service GMUG, SJ-RG, PISCC. 1999. TES Plant Management Strategy, Grand Mesa, Uncompahgre and Gunnison, San Juan, Rio Grande, Pike-San Isabel National Forests and Comanche-Cimarron National Grasslands. Five year action plan 1999 to 2003. U.S. Forest Service, Denver, CO.
- U.S. Bureau of the Census. Undated. Negative Population Growth State Facts – Colorado. Source: U.S. Bureau of the Census. Internet site: <http://www.npg.org/states/co.htm> [Accessed June 2003].
- U.S. Census Bureau. 2001. Source U.S. Census Bureau: Data derived from Population Estimates, 2000 Census of Population and Housing, 1990 Census of Population and Housing. Last Revised: Wednesday, 07-May-2003 16:44:21 EDT. Internet site: <http://www.census.gov/> [Accessed June 2003].
- U.S. Environmental Protection Agency. 1997. Climate Change and Colorado. EPA 230-F-97-008f. Office of Policy, Planning and Evaluation, Climate and Policy Assessment Division, Washington, D.C.
- University of Michigan Herbarium. Type collection of vascular plants. Holotype *Oenothera harringtonii*. Last Updated: 31 January 2002. Internet site: <http://herbarium.lsa.umich.edu/> [Accessed February 2003].
- Wagner, W.L. 1983. New species and combinations in the genus *Oenothera* (Onagraceae). *Annals Missouri Botanical Garden* 70:194-196.
- Wagner, W.L., R.E. Stockhouse, and W.H. Klein. 1985. The systematics and evolution of the *Oenothera caespitosa* species complex (Onagraceae). *Monographs in systematic botany from the Missouri Botanical Garden* 12: 1-103.
- Weber, W.A. and R.C. Wittmann. 2001. Colorado Flora – eastern slope. Third edition. University Press of Colorado, Boulder, CO.
- Welsh, S.L., N.D. Atwood, S. Goodrich, and L.C. Higgins. 1993. A Utah Flora. Second edition. Brigham Young University, Provo, UT.
- Werner, P.A. and H. Caswell. 1977. Population growth rates and age vs. stage distribution models for teasel (*Dipsacus sylvestris* Huds.) *Ecology* 58:1103-1111.
- Wittmann, Ronald C. 2003. NIST, Boulder, CO. Personal communication.
- Wootton, E.O. and P.C. Standley. 1913. Descriptions of new plants preliminary to a report upon the flora of New Mexico. *Contributions from the United States National Herbarium* 16 (4):109-196.
- Zeevaart, J. 1981. Botany and Plant pathology Department, Michigan State University, East Lansing Michigan. Personal communication.

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